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BREEDING, FEEDING, AND OTHER LIFE HABITS OF MEADOW MICE (MICROTUS)[1]

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INTRODUCTION

The meadow mice, field mice, or ground voles, of the genus *Microtus* (*2*),[2] comprising numerous species and geographic varieties, are widely distributed throughout Europe, Asia, and North America, mainly in Temperate and Boreal Zones. Comparatively few species live in the Tropical or Lower Austral Zones, but many range north far beyond the Arctic Circle. Their greatest abundance and importance, however, is in the middle zones, the region of greatest agricultural production.

These rodents are all small or of medium size, with a stout compact body, short legs, short tail and ears, small eyes, soft fur, and dull colors, as becomes ground dwellers and habitual burrowers into the earth. Some are semiaquatic, living in marshes or along the banks of streams; others occupy the meadows, uplands, and even the semiarid parts of our desert areas. With this wide range of adaptation one or two, or sometimes three or four, species in a locality occupy most of the fertile areas of the United States and Canada, where they become of economic importance as farm and orchard pests (*4; 5, p. 121–123; 9, p. 97–102; 10; 12; 20*).

MOUSE PLAGUES

In the Old World, meadow mice have for centuries presented serious agricultural problems, suddenly appearing in vast hordes that devoured the crops over extensive areas and causing heavy losses and much human suffering. Full accounts of these mouse plagues, which have appeared in Scotland, England, France, Germany, Italy, Greece, Hungary, Russia, Siberia, and Kamchatka, have been published.[3]

In our own country there are constant waves of abundance and diminution in numbers of meadow mice, not country-wide, but rising and falling locally like swells of the ocean. These are noted in frequent complaints of unusual damage to crops or fruit trees by mice in different parts of the country, and some of the higher waves have been designated as mouse years or mouse plagues (*16*).

One of these waves occurred during 1907 in the Humboldt Valley, Nevada (*16*), a rich agricultural area then under irrigation and supporting enormous areas of alfalfa that would yield two or three heavy cuttings a year with an aftermath for pasture during a part of the mild

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[2] Reference is made by number (italic) to "Literature cited," p. 534–535.

[3] For references to accounts of mouse plagues in Old World countries, see list of literature in Lantz's report on field mice (*11, p. 64*).

winters. The ranches were large, mainly from 500 to 1,000 acres each, and some with as many as 4,000 acres. Cultural methods were lax at the time, and ditch banks, fence rows, and roadsides were a tangle of dense vegetation that remained uncut throughout the year.

Under this wealth of cover and with the rich food of alfalfa, the native meadow mice (*Microtus montanus*) became abundant during the fall of 1906, but were little noticed. By the early summer of 1907 the fields were full of them and only half a crop was harvested in the June cutting, and in August still less, and over whole ranches none. In the valley below Lovelock, Nev., crops and orchards had been destroyed or seriously injured, and many of the fields were bare of vegetation in November, 1907, and the millions of mice were digging deep into the ground for the alfalfa roots. In some of the fields there were literally thousands of mice to the acre.

The money loss to farmers from mice in that part of the valley was conservatively estimated at a quarter of a million dollars. Mice were also reported as very numerous and destructive to crops in the Carson and Paradise Valleys and at other points farther up the Humboldt Valley, but these areas were not included in the estimates of losses. A similar outbreak of these mice was reported by the ranch owners in 1899 and 1900, with almost as heavy losses as in the one cited.

A poisoning campaign was instituted by the Biological Survey of the United States Department of Agriculture under the expert supervision of Stanley E. Piper. The farmers combined to distribute poisoned food until the numbers of mice were reduced to a point where the situation could be controlled by their natural enemies, the coyotes, foxes, bobcats, badgers, skunks, weasels, owls, hawks (*7, 8*), ravens, crows, magpies, gulls, herons, and shrikes, which had congregated in unusual numbers to feast on them. By the next spring the mice were scarcely more numerous than usual. Their food supply and protecting cover had been consumed during the winter and reproduction had diminished while their enemies multiplied.

STUDY OF HABITS

To understand more fully the underlying causes of such rapid increases in numbers of these rodents, which are referred to generally in the literature dealing with field mice (*1, p. 341–346; 6, p. 292–299; 13, p. 174–177; 14, p. 403–406; 15, p. 275–276; 17, p. 186–191; 18, p. 97–101; 19, p. 515–537*), the Biological Survey has undertaken studies of the breeding and feeding habits of the common eastern representative of the group, *Microtus pennsylvanicus*, which with its subspecies covers over half of the continent of North America. To recount these experiments in detail would be tiresome and needless, for the general results are sufficiently startling in significance and practical application.

GENERAL HABITS OF MICROTUS PENNSYLVANICUS

The Pennsylvania meadow mice are primarily meadow dwellers. They are capable, however, of adapting themselves to almost any situation where a choice food supply is obtainable, and live in flooded marshes where they are forced to swim from one dry spot to another, cross small streams, or even range out over dry uplands in fields or orchards. They are active throughout the year; in winter, with thick fur coats, enjoying the restricted life under the deep snows in the north as much as their greater freedom with its increased dangers in summer. They dig nu-

merous shallow burrows in the ground, connected by a network of tiny roadways under the old grass and fallen vegetation, which protects them from the view of overhead enemies; build soft clean nests of fine grass and plant fibers under or on the surface of the ground, and in these nests raise their large families of young, and generally live a sociable, communistic, primitive type of animal life. While not highly endowed with even rodent intelligence, they are quick to adapt themselves to the food supply that is available, to the best possible means of protection from enemies, and to make the best of what, from the point of view of even a squirrel, might seem a very humble existence.

VOICES

Meadow mice are by no means dumb, as some have asserted, though to our gross ears they may seem so. The young have many forms of minute whimpering, whining, crying sounds which seem to have a meaning to their mother. As she leaves the nest, and perhaps interrupts their meal, there is a fine little complaining jumble of whimpers from the very young, to which she pays no attention. If one tumbles out of the nest and lies wriggling helplessly on the floor it cries with a vigor that brings a quick parental response and is carried back and replaced in the nest. If it falls far enough to be slightly hurt but not to be greatly injured a sharp squeal of pain sets the mother frantic to find and help it.

The adults and the older young have little talky squeaks and sharp cross squeaks and savage squeals, and in a fight a blur of squeaks and squeals and guttural growls, not far different from a dog fight on a very small scale. Then there are chatterings of teeth at each other and stampings and scratchings on the ground when rivals meet, all of which, and probably much more that we miss, have an evident meaning to them. A stranger or friend is recognized, either by voice, odor, sight, or other token, as quickly as we recognize a friend or foe.

DISPOSITIONS

In their home life these mice are sociable, friendly, playful, and happy among the members of a well-fed family or colony, but are savage fighters in the case of rival males or of females in defense of young, or among strangers. When hungry or without comfortable nests or living conditions, they become cross and quarrelsome, will fight among themselves, even to the death, and will eat those killed, especially the young.

They are fond of meat at any time, have no scruples against cannibalism, and will generally kill and eat newly born young not protected by the mother. Being ready fighters and always on the defensive, they will usually bite anything that catches or touches them, but can be safely handled, either by catching them firmly in the hand from above or by letting them run over the hands or arms or from one hand to the other. They are not easily so tamed as to be gentle and safe to play with, but, unlike many of the native mice of other groups, are not timid and nervous.

INDIVIDUALITY

There is great individuality, however, in dispositions and habits, some mice being comparatively timid and nervous, while others are more gentle and confiding, seeking rather than avoiding notice. Some are

very fond of certain foods which others have not learned to like or will not eat. Some individuals are very talkative, always squeaking or making some noise at the others, while more of the individuals are quiet and generally silent. Some are far more pugnacious than others and often bite if handled, while others may be held in the hands and stroked without offering any resistance. These differences are noticed in the young just beginning to run about, and seem to be to some extent inherited characteristics. Certain pairs will live together in perfect accord, while others will quarrel and fight and refuse to occupy the same nest. Some females will accept the attentions of only one male and will savagely resent the advances of all others, while others show no preference and will accept attentions promiscuously.

Most of the males are highly polygamous, but one pair that lived together until after the young were born were from the first very affectionate, remaining much of the time together in the nest box and paying little attention to the mice in neighboring cages. This male would not voluntarily leave his cage nor enter the cage of another female, even when called. This was very unusual, as most of the males were eager to go into other cages and make friends with the females or fight with the males.

In No. 6 cage a male and female had lived contentedly together and raised two families of young, while against their cage an old female lived alone in No. 3 and was on friendly terms with her neighbors through the wires. After she had given birth to her fourth family of eight young she was making her peculiar squeaking calls, which the male in the other cage evidently recognized as an invitation to visit her, and as he eagerly came up over the edge of his cage and down into hers the female in cage No. 6 became greatly excited and twice forced her way out under the roof of her cage and tried to get into cage No. 3 to punish her rival. Not being allowed to do this she stormed around her own cage, squeaking, kicking up the sand on the floor, biting the wires, and showing every indication of rage until her mate came home in the evening. Then she pounced upon him, bit his nose, chased him around the cage, squeaking and scolding at him until he was severely punished. She was cross with him all the evening, but the next day had settled down to her usual pleasant frame of mind and had evidently forgotten her domestic troubles.

A neighboring male that came into cage No. 1 during the mating time of the old pair that had been captured in their wild state was pounced upon by the female and his foot so badly bitten that he was glad to escape to his own cage and nurse his bloody paw. In other and the majority of cases the females made no objection to their mates visiting other females as much as they wished, and these two cases are exceptions to the usual free-love manner of life among these polygamous little animals.

These incidents, however, show variable tendencies in the social life of the meadow mice, which, under certain conditions of environment, might lead to perfect monogomy if for any reason this should prove beneficial to the species.

PLAYING

With such quick and energetic little animals it is sometimes difficult to distinguish between work and exercise and mere play. The young, soon after their eyes are open, will push and pull and roll each other about in unmistakable sport and up to half-grown size are conspicuously

playful, but the vigorous exercise of the older animals seems more like the necessary release of superabundant energy, or sometimes an expression of nervous excitement. In the cages they get abundant exercise and apparently much enjoyment from running in their hollow revolving wheels or around on the inclined disks, sometimes two running side by side in a wheel, or two to five running together at high speed in perfect time and step on a rapidly revolving disk. They soon acquire great skill in jumping off and on without checking the motion of the disk, and if the motion is checked they may all reverse and start at full speed in the opposite direction. In a cage with a large number of occupants the wheel is kept going much of the time both night and day, even by old and fully grown animals, but with one or a pair in a cage, the early morning and evening are the busy hours for exercise, or play, as you choose to call it.

FIGHTING

In their own families and among their own friends meadow mice are generally friendly, playful, and even affectionate, but there are times when with strangers, rivals, or intruders they are vicious little savages. The mother will fight anything from another mouse to a bulldog or a man in defense of her young. Possession of a cage, a nest, or a favorite corner is sometimes the cause of a quarrel, of squeaky disputes, or even a fight in which the intruder generally yields and retires. The mating of a strange male and female often begins with several little fights in which the male sometimes gets a bloody nose, while the female seems never to be injured, but usually after a few minutes they are fully mated and the affair has passed as a mere formality of microtine etiquette. If the female is not ready for mating she may keep up attacks on the male until he is forced to retire to a corner and nurse his injured feelings, if not an injured nose.

The real fights are among rival males and usually males from different families, and these are apt to be serious or sometimes fatal. One nearly full-grown male that by mistake was dropped into the cage with an older and larger male was nearly killed in a few minutes before it could be rescued. Both fought savagely and so fast that their motions were a complete blur, so that nothing could be seen of their methods of attack. When separated, the smaller one was found to be so badly injured that he was killed and his skin and skull saved for a specimen. He was bitten around the head, on the back, belly, feet, and tail, two large gashes were cut across the abdomen, and the skin of the back was so full of holes that it looked like a shotgun target. He would have been killed in a very short time if left in the fight. The larger male seemed stiff and sore for a few days, but recovered from his injuries. Occasionally, a male is trapped in the meadows with his skin cut full of holes from a fight, in which case he may be safely assumed to be the sole survivor of a fatal combat.

SANITATION

Like most wild animals, meadow mice are as neat and cleanly in habits as circumstances permit. Although often digging in the earth and running through the mud they also run through shallow water and swim and dive on occasion. Their fur is fairly waterproof and when wet quickly dries as it is carefully combed and cleaned. After working in the earth the mice clean their nails and comb their fur, which they

usually keep in perfect condition. Without plenty of water or dry earth the fur becomes oily and rough, but either water or sand removes the excess oil and leaves it light and fluffy.

The nests are kept clean while in use and are abandoned when they get old and stale. New nests with soft linings are usually prepared a few days in advance for each litter of young, so that new nests or fresh linings are generally provided about every 20 days.

Their little long green pellet-like excrements are more or less scattered along the trails and on the feeding grounds, but in the burrows or near the nests they are deposited in little heaps in out-of-the-way places. In the cages some corner farthest from the nest is usually chosen for the purpose, or sometimes the water dish is used as a urinal and the pellets are deposited in a corner or in another dish. In such case to keep the cages from becoming foul they have to be cleaned frequently and supplied with fresh sand or sawdust. As an experiment, outside receptacles were provided by placing a square tin can with a hole in the side large enough for the mice to enter from a corresponding hole in the side of the cage. An inch of sand in the bottom of this can gave an attractive little dark compartment which the meadow mice at once adopted and used exclusively for toilet purposes. As the cans merely hooked onto the outside of the cages and could be conveniently emptied and supplied with fresh sand every day or two, the cages were kept clean with little trouble.

BREEDING HABITS

It has long been known that these mice are very prolific breeders, specimens of females containing embryos, usually four to eight in number, being taken at all seasons. The mammae are arranged in four pairs, two of inguinal, and two of pectoral on four elongated mammary glands, and eight young should be the normal maximum number.

FREQUENCY

In captivity the young, if well fed, begin to breed when less than half grown, the females mating with older males when only 25 days old and having young when 45 days old, and the young males mating when only 45 days old. The period of gestation is approximately 21 days, in one case 20 days and 17 hours. The breeding activities are practically continuous, the females mating immediately after the birth of the young and producing litters of usually 4 at first, but when full grown, after the first or second litter, usually 6 or 8 at a birth. Seventeen consecutive litters of young have been produced by one female in captivity within a year—May 25, June 14, July 8, July 29, August 23, September 18, October 18, November 9, November 30, December 21, January 12, February 2, February 23, March 18, April 8, April 30, May 20—and then she showed no signs of being near the end of the breeding period, while several generations of her young have busily followed her example, one of them, born on May 25, having produced 13 families of young, totaling 78 in number, before she was a year old.

The number of young in a litter ranges from 2 to 9, and with the original pair, averaged 5, totaling 83 in 17 litters. At this rate of increase, allowing equal numbers of males and females and the young beginning to breed at 46 days old, the total increase from one pair, if all lived and bred, would be over 1,000,000 individuals at the end of a year. If all

these were confined to one acre of ground, this would mean a little more than 20 mice to every square foot.

MATING

"Mating" is only for the immediate needs, and a misnomer at that, because a female usually accepts the attention of any number of males in rapid succession and shows no choice of individuals, favor to young or old, or any regard to relationship, whether sire or brothers or previous offspring. There seems to be no moral necessity of life with them other than the most rapid increase possible of individuals of the species. The one exception to complete promiscuity is provided by nature in the slower sexual development of the males, which prevents inbreeding within the litter before the young have scattered, the males not coming to sexual maturity until about the time the first young of the females of the same litter are born. Furthermore, respect for the females during pregnancy by even the most virile old males is enforced with such spirit that it seems never to be questioned.

When a half-grown female jumps and squeaks at an old male, he cringes or runs, for he knows that her teeth are sharp and that she will not hesitate to use them. If he comes too near her newly born young, the mother will sometimes punish him severely before he can get out of reach. If the very young are left unguarded, the males or other members of the family will often kill and eat them or sometimes wantonly bite and kill them all before their mother returns. In crowded cages it is difficult to prevent the young from being killed, but the mother is a model of care and solicitude, ready to fight to the last for them and to use all her intelligence and energy in their protection.

NESTS

The female builds a new nest for the reception of the young, endeavoring to place it where none can find it, but if discovered and disturbed she promptly removes the young to a place of safety. If suddenly alarmed she often rushes out with all of the young clinging for dear life to her nipples and drags them for some distance along the runway or under cover, where she can gather them and carry them one at a time in her mouth to another nest. So quick and shuttlelike are her motions that the young disappear as if by magic, and when one nest box is disturbed the young will all be found a few moments later in another.

In cold weather the nest is built especially thick and warm, and the newly born young are not left for more than a few moments at a time, and then the mother covers them up securely before she leaves them.

One old mother in No. 3 cage had a new family one cold night in March. In the morning she was very hungry for her breakfast when it was placed in the cage, but was greatly worried about the young getting cold if she left them for a minute. She rushed out of the nest box and back several times without stopping to eat, and seemed greatly disturbed. Suddenly she rushed up to her one remaining young of the previous litter, then 22 days old, well furred and nearly half grown, seized it in her mouth and carried it into the nest, and leaving it with the tiny naked babies, returned to the food. The foster mother soon reappeared at the breakfast table but was instantly grabbed up, rather roughly, and with many squeaks carried back into the nest, where this time it remained while the real mother finished her breakfast.

CARE OF YOUNG

The young are hairless and weigh only about 3 gm. each when born, with closed eyes and ears and no trace of teeth. They grow rapidly, however, gaining after the first few days about 1 gm. a day until over half grown. Their dark-colored fur begins to appear as soft velvet in five or six days, their incisor teeth about the fifth, the molar teeth about the seventh, and their eyes and ears open on or near the eighth day. As soon as their eyes are open they are quick to run and hide if disturbed, and a few days later are out of the nest searching for food, following the trails, and, if in cages, running on the wheels, playing and pushing for their rights.

When about 12 days old, the young are weaned, but they remain with their mother, occupying the old nest and holding together in friendly family relations until time for the next installment of young, when the mother seeks or builds a new nest and leaves her previous family to care for itself. If food were abundant, they would remain contentedly together for an indefinite time but for the disturbing sexual forces which before they are full grown impel the females to seek new homes for prospective offspring and the males to wander constantly in search of one mate after another.

FACTORS MODIFYING BREEDING

Factors modifying breeding activities are food, weather, cover, proximity, and contentment. A group of 9 mice, 5 females of breeding age and 4 males, kept in roomy cages and starved for 36 days until hungry, thin, cross, and squealing like half-fed pigs, showed no signs of breeding until at the close of the period when the quantity and quality of their food had been brought up to a satisfying point. The females, fighting the males away, kept them constantly cowed and in fear of their lives and actually killed and partly ate one old male, the largest animal in the cage. They also killed and ate one quarter-grown young at the time when famine was sorest. As their food was increased and changed to more nutritious quality the females rapidly yielded to male attention and all were quiet and contented again. Even for this short period, others in cages where well fed had raised one family of young and had the next well under way. It seems highly probable that a natural shortage of food in a dry year or some other cause might retard breeding for a much longer or for an indefinite period. The three litters of young afterward born to the starved females numbered only 3, 4, and 5, while at the same time, in cages well supplied with food, 5, 6, and 8 were the usual numbers.

Weather apparently has an effect on the rate of breeding, for while under certain conditions the mice breed in winter, their breeding activities are generally much retarded then or entirely suspended. Of great numbers of specimens collected at all seasons of the year, few females are found to contain embryos in winter except in warm southern climates or where there is unusual protection. In Minnesota tiny naked young are sometimes found in nests under haystacks in midwinter, but in less sheltered localities with only the normal winter food they are rarely found. While the reduced winter food supply may be partly responsible for the general suspension of winter breeding, the excessive cold seems undoubtedly a potent factor. The continuous hot weather of the Tropics

seems to be a bar even to the existence of the mice, but in the Temperate Zones they breed continuously through the warm seasons.

Cover, or some secure place in which to construct the nests, seems necessary for favorable breeding conditions or for the contentment of the animals. In fact, where not protected from overhead enemies by some concealing screen of vegetation or other cover they are soon exterminated.

Scarcity of individuals may often tend to retard or entirely to check reproduction. The mice may be left stranded out of reach of mates, when breeding perforce ceases until stimulated by a gradual influx from other localities.

Discontent with environmental conditions, nature of soil, lack of water, terror of enemies, or any other disturbing elements might well prevent breeding and scatter the individuals. A change from an old cage to a new and better one will sometimes cause several days of unhappiness, struggle and effort to escape, gnawing at the wires, frantic running round and round the walls, impatience and snappishness with each other, and especially a savage attitude of females toward the males.

On the other hand, breeding is evidently stimulated by rich food, mild weather, safety, quiet, sociability, comfortable living conditions, and general contentment. How far this would continue without degeneration of the vigor of the species has not been determined, but for a time at least the stimulating effects of abundance and prosperity are pronounced.

FOOD HABITS

In their native habitat meadow mice feed to a great extent on grasses and sedges, selecting the tender new shoots in spring, the inner hearts at the base in summer, the green and ripening seeds in summer and autumn, and the tender bases, dormant sprouts, roots and root stalks, bulbs, tubers, and the bark and buds in winter. They feed also on the clovers and a great variety of meadow and upland plants, eating both the green tops, flowers, and seeds, and the roots.

In times of scarcity, especially in winter and under protection of snow, the mice eat the inner bark and tender cambium layer from shrubs, trees, and vines, often completely girdling the trunks as high as they can reach above ground and stripping the roots well below the surface.

In fields, gardens, orchards, and home grounds the mice show a fondness for grains of all kinds, most garden vegetables, and the bark of many fruit and ornamental trees, shrubs, and vines. Often they cut down and destroy and waste far more growing vegetation than they eat.

STORES

In times of abundance, and especially in autumn, food is stored for future use. Along the upper Missouri for ages Indian tribes have gathered part of their winter food by robbing the mouse stores of ground beans, artichokes, and other tubers. Several quarts or a peck of these beans and tubers are often taken from a single cavity, and a person can sometimes gather several bushels a day from the mouse stores (3). In other parts of the country various roots, tubers, and bulbs are stored. In captivity the mice will often secrete all surplus food under or near the nest, sometimes filling their nest boxes full of seeds, grains, and vegetables. In cold weather when the young are about to be born, the mother stores up all spare food and places it around the nest where it can be

reached without her leaving the delicate, naked young or exposing them to the cold. Approaching maternity may often be noted by this habit.

IN CAPTIVITY

In captivity mice will eat a great variety of green vegetation, but they show an especial fondness for all of the clovers and other legumes. Grass is extensively eaten, but does not satisfy them so well as clover, and is always left if abundance of both are fed together. Mice are especially fond of cantaloupes, completely devouring the rinds left from the table. Green corn is one of their favorite foods, and even the cobs are picked bare to the core. Most vegetables are eaten with more or less relish, as well as all grains and seeds, bread, fruit, fresh meat, fat, or bacon. Rolled oats seems to be a favorite food with both young and old.

Like all their vital processes, feeding and the elimination of waste are very rapid. The animals apparently eat every few hours all day and all night, and the accumulations of pellets in the corners of the cages grow rapidly.

QUANTITY OF FOOD REQUIRED

The quantity of food eaten is astonishing. In one cage, 30 days' feeding of 10 mice with all the clover, cantaloupe, grain, and seeds they would eat showed, after deducting 10 per cent for waste which could not be otherwise accounted for, that an average of 55 per cent of the weight of each animal was eaten every 24 hours. This was on the richest kind of food, such as they rarely obtain in the wild state.

In another cage during the same period nine that were fed grass, clover, and cantaloupe rinds, with no grain or seeds, ate, after deducting 10 per cent for waste, an average of 107 per cent of their weight every 24 hours. This would seem more nearly their normal ration in a wild state and the best basis for computing food consumption. Some days they ate nearly twice their weight in green food, but only after they had become unusually ravenous. In both cages they had revolving wheels on which they exercised vigorously and were living fairly normal, contented lives.

In one cage the average weight of the animals was 30 and in another 33 gm. a part of the animals being immature. The adults average about 50 gm. but 30 gm. would be a fair average for the general run of young and old meadow mice in the field.

AGGREGATE DESTRUCTIVENESS

At 30 gm. a day one meadow mouse would consume 10,950 gm. (23 pounds) of green food in a year, and 100 mice 2,300 pounds, or a little over a ton of green grass or clover, which would make about half a ton of dry hay.

A hundred mice to an acre is not an unusual number in meadows favorable to theirhabits, while in "mouse years" or during mouse plagues, the number has been estimated at thousands to the acre. Even with 1,000 to the acre it is easily shown that mice consume more vegetation (11½ tons) than would ordinarily grow on an acre in a year.

Mouse plagues, disastrous as they are locally, are of minor importance in comparison with the steady yearly drain on crops by the mice over the country at large in normal years. Even as few as 10 meadow mice to the acre on 100 acres of meadow would take about 11 tons of grass, or 5½ tons of hay, a year. Or this number on the 65,000,000 acres of hay raised in the 38 mouse States [see "Monthly Crop Reporter," p. 153, 1921 (*21*)], would cause a loss of over 3,000,000 tons of hay a year, or a money loss of some $30,000,000 annually in hay alone.

Of other crops, grains suffer most from the ravages of meadow mice, especially when left long in shocks or stacks after harvest and in situations where accessible, but from the seed and sprouting grain to the ripened crop all grains are eagerly eaten. Small fields are likely to suffer most, as the mice penetrate less readily to the middle of large cultivated areas.

Root crops and vegetables are sometimes injured by meadow mice, but usually not so seriously as by the more exclusively burrowing pine mice (*Pitymys*). In times of great abundance of the mice, however, they have been known seriously to injure the potato crop and almost to destroy many garden vegetables.

Destruction of fruit trees and many ornamental trees and shrubs in winter by the mice eating the bark from the base of the trunks, often completely girdling and eventually killing them, causes more annoyance than any of the more serious and less conspicuous losses. This is usually done under cover of deep snow with no indication of harm until the snow has disappeared in spring. Many fine orchards have thus been seriously injured or completely ruined.

METHODS OF CONTROL

The importance of keeping these mice under control and at a minimum number is clearly seen. Much has been published on their habits, depredations, and the most economical methods of destruction, and the appended references are to papers that cover this phase of the subject: *4; 5; 9, p. 97–102; 10; 11; 12; 16; 18, p. 97–201; 19, p. 515–537; 20.*

The most economical and practical method of control, that is, control by natural enemies, has been given least emphasis. In his studies of the food of hawks and owls (*7, 8*), Dr. A. K. Fisher has shown the great value of these birds in reducing the numbers of meadow mice, but the value of many other birds which feed upon them—gulls, terns, herons, bitterns, cranes, ravens, crows, magpies, shrikes, jays, and others—has not yet been fully recognized. The enormous consumption of these mice by skunks, minks, weasels, martens, badgers, foxes, coyotes, bobcats, lynxes, and even bears can not fail to have a marked influence on their abundance. To what extent they are preyed upon by shrews and flesh-eating rodents is not fully known. Snakes and even fish help to keep them under control.

The mouse problem involves more than protecting the enemies that are otherwise not too obnoxious; it means giving these enemies a chance to see and catch the mice, at least at the borders of the fields and meadows, and along the roadsides. Simple cultural methods, that would pay for themselves in the reduction of weeds and in added beauty of landscape, would remove the permanent cover that makes it possible for the mice to persist in otherwise well-cultivated areas. Clean fields and meadows, and clean borders, roadsides, and ditch banks, would help to solve the

problem of mouse control, prevent occasional heavy losses, and add considerably to the yearly farm returns.

USES

Total extermination of meadow mice, even locally, would be as impossible as it would be undesirable. These rodents are firmly intrenched in the waste places of the earth where they do no harm and may do some good. Then, too, they have a value, even from our narrow and selfish point of view. Seton has called them "the boats especially designed to bring over food from the Mainland of Grass to the Island of Carnivores," and they certainly are largely instrumental in supporting many of the animals that provide us with warm furs. They are also the daily bread of numerous birds of prey that agriculture could not well spare without great danger from other rodent pests. To some of the native tribes of America they still supply an important part of the winter vegetables from their winter stores of ground beans, tubers, and roots (*3*).

More than any other group of small mammals, meadow mice hold the key to the balance of natural adjustment for a large portion of our native bird and mammal population. They have also a vivid lesson for us in the struggle of life, the surge of dynamic biological force against the shores of relentless destruction, a fierce struggle for existence, which, through highly perfected adaptation to environment, has won a well-balanced coordination of body, mind, and morals that serves the best end for the perpetuation of the species.

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PLATE 1

A.—The original female used in the studies described, weighed when captured, April 1, 1922, 32 gm. On August 20, just before the birth of six young, she weighed 70 gm., and after their birth 54 gm. On May 20, 1923, just before the birth of six young she weighed 105 gm., and after the young were born 80 gm.

B.—The old male when captured, April 1, 1922, weighed only 36 gm. On August 6 he weighed 56 gm., and on May 20, 1923, 72 gm. Another male born on May 25 weighed when a year old 81 gm.

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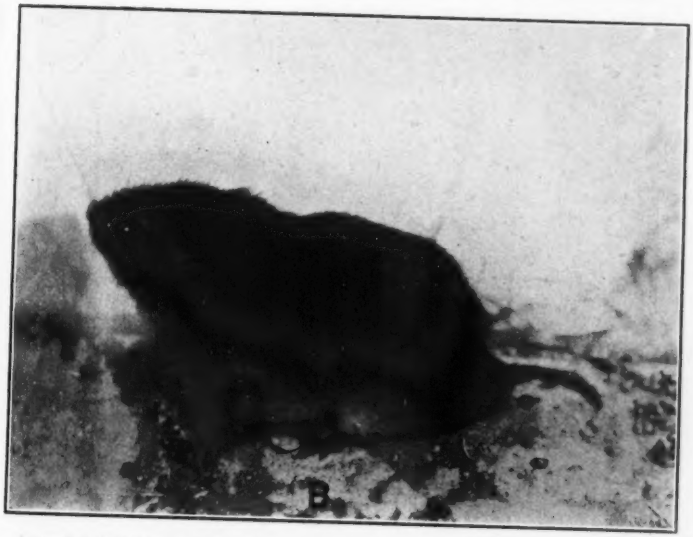
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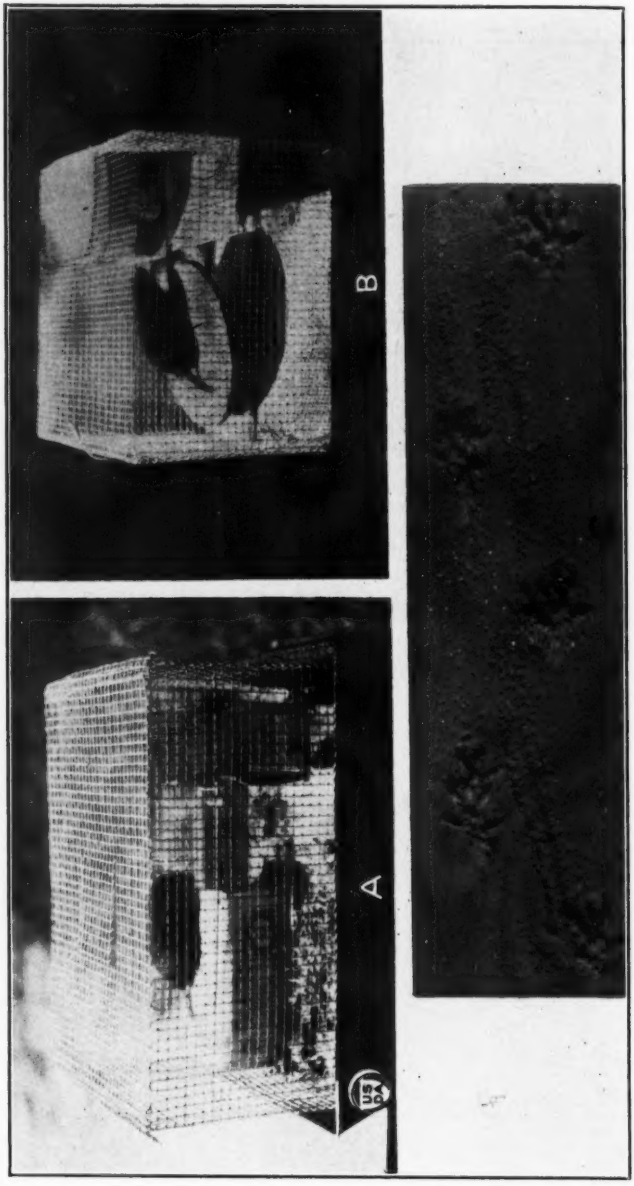
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PLATE 2

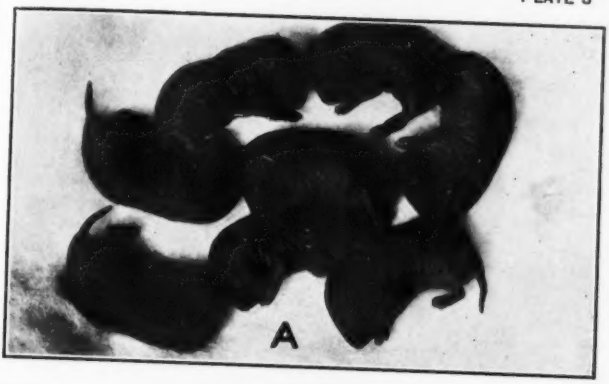
A.—A simple wire-mesh cage in a sand pan, with nest box, food and water dishes, and a vertical hollow wheel for exercise, makes comfortable quarters for mice and is easily cared for. The top is hinged so as to open upward.

B.—A small, quarter-inch wire-mesh cage containing nest box and water dish on shelf, a revolving disk for exercise, and sand and food dishes on the floor, will accommodate one mouse very comfortably and can be connected by side doors with other cages.

C.—Tracks of a meadow mouse trotting over a thin layer of white flour; about natural size.

PLATE 3

A.—Young just born.
B.—Young four days old.
C.—Young seven days old just before the eyes and ears open.
The young at birth are naked, blind, toothless, and helpless, weighing only about 3 gm. each, but they grow rapidly. All about natural size.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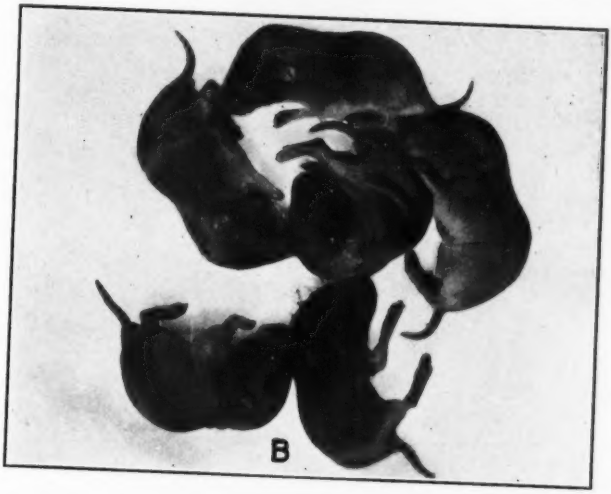
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C

INHERITANCE OF THE CRINKLY, RAMOSE, AND BRACHYTIC CHARACTERS OF MAIZE IN HYBRIDS WITH TEOSINTE[1]

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INTRODUCTION

To be of maximum efficiency, plant breeding must deal with all existing wild relatives of the plant being bred, for it is only in this way that investigators can take advantage of special characteristics acquired through ages of evolutionary progress. Zea is a monotypic genus, and its nearest wild relatives are the two species of large Mexican grasses, *Euchlaena mexicana* and *Euchlaena perennis*, commonly known as teosinte. As a first step in ascertaining the possibilities of combining the desirable characters of maize and teosinte it is essential to determine the hereditary behavior of hybrids between them. Progress in this direction was reported by Collins and Kempton in the analysis of a hybrid between Tom Thumb pop corn and *Euchlaena mexicana* (*5*).[2] In this hybrid there was seemingly complete blending of maize and teosinte characters; it became of interest, therefore, to analyze the behavior of some of the more strictly Mendelian variations of maize in hybrids with teosinte. The present paper reports the inheritance of three striking Mendelian characters of maize, crinkly, ramose and brachytic, in hybrids with the annual teosinte, *Euchlaena mexicana*. The inheritance of these three variations in maize hybrids is now fairly well understood, all three behaving as simple Mendelian characters recessive to the normal form.

The great variability of maize has become a byword. Each year sees the discovery of a new series of true breeding teratological forms, embracing almost every part of the plant, leading to the belief that the number of different sorts is infinite. In fact, so numerous are abnormal forms that improvement in maize has become centered largely on the problem of eliminating deleterious mutations from existing varieties.

In view of this abundance of variations in maize it seems rather surprising that its nearest wild relative, *Euchlaena mexicana*, is unusually free from true-breeding abnormal variations. Although more self-fertilization probably occurs in Euchlaena than in maize, there is enough cross-fertilization to permit degenerative recessive variations to survive as heterozygotes, so that the difference in stability hardly can be ascribed to the relatively greater homozygosity of Euchlaena.

Crosses between Florida teosinte, *Euchlaena mexicana*, and most of the well-known Mendelian variations of maize are being made as opportunity offers, as well as crosses between these variations and the perennial species *Euchlaena perennis*. The two species of Euchlaena seem to react differently in hybrids with maize, and the first generation

[1] Received for publication Sept. 8, 1923.

[2] Reference is made by number (italic) to "Literature cited," p. 596.

of hybrids with the perennial species shows a much higher degree of dominance of all the characters of teosinte than has been found in hybrids with the annual species.

At the present time, F_2 populations have been raised from crosses of *Euchlaena mexicana* with golden (*13*), ramose (*9*), brachytic (*10*), rainbow (*1*), and crinkly (*7*), while F_1 progenies have been grown with dwarf (*6*), and pod (*14*).[3]

In making these hybrids teosinte almost invariably is used as the female parent, since in controlling the flowering stage of this species by shortening the length of day, the staminate flowers are suppressed. As teosinte has but from 7 to 10 seeds in each pistillate spike, only a few seeds are obtained as the result of each pollination; the first-generation populations therefore are small. In the crosses with crinkly, ramose, and brachytic maize, however, teosinte served as the male parent; with the crinkly an unusually large number of seeds were obtained, in consequence of which a large F_1 population of this hybrid was grown.[4] The hybrids differ somewhat in general vigor and in the size of the plants, one of the most vigorous being the crinkly cross, which seems to have commercial possibilities as a forage plant. In the character of the inflorescences, all resembled the hybrid with Tom Thumb, with the exception of the cross with the dominant variation pod. This, as was to be expected, produced long glumes on the pistillate spikes similar to those of a podded ear. These long glumes on the characteristic four-rowed ear of the F_1 maize-teosinte hybrid give a rather startling resemblance to a gigantic wheat head (Pl. i).

The hybrids with golden and rainbow, of course, were normal with respect to these characters, and segregated in the F_2 into numerous grades of the parental colors.[5] In a population of 371 plants of the rainbow cross no plants as fully variegated as the maize parent were recovered, though many truly beautiful plants were produced.

In the hybrid with golden, plants were obtained fully as yellow as the parent, if not more so, though there was no clear distinction between golden and green. The segregation in the F_2 of these hybrids suggests that Euchlaena possesses modifying factors for both of these characters and, as in other hybrids, the form of inflorescence seemed to be associated but loosely with the Mendelian characters under observation.

The inheritance of the other three characters, crinkly, ramose and brachytic, is capable of quantitative analysis, which should offer more critical evidence on the existence in *Euchlaena mexicana* of modifying factors for these characters.

[3] Seed stocks of golden and crinkly were received from R. A. Emerson, ramose from W. B. Gernert, pod from H. S. Sconce, while rainbow was purchased from Luther Burbank and brachytic and dwarf arose in our own pedigreed stock. The degree of yellow in the original golden strain was somewhat variable, but the strain finally used in the cross with Euchlaena was developed from the original stock with rather an extreme expression of the yellow pigment. The stock of rainbow purchased from Burbank has well-developed white and yellow stripes, together with the red plant color. The inheritance of the japonica striping has been reported by Lindstrom (*13*), while that of red plant color has been reported by Emerson (*8*). The stock as originally received was heterozygous for red plant color and for yellow as opposed to white striping. The degree of expression of all of these characters was variable, though no self-colored plants have been found in the original stock. Through selection and inbreeding it has been possible to isolate lines having almost chlorophyll-free upper blades, and others practically self-green. The seedling leaves of these divergent strains are very similar, perhaps the only difference being the rather earlier appearance of variegation in the extreme white strains.

In the cross with Euchlaena a medium-variegated plant was used, being homozygous for red plant color and heterozygous for white and yellow stripes.

[4] These crosses were made by C. G. Marshall at Chula Vista, Calif., and the F_1 and F_2 populations were grown under his direction at the same place.

[5] The F_1 plants of the hybrid with rainbow were red, as was to be expected, but were normal in that the striped condition of rainbow was completely recessive.

The fact that these teratological characters can be recognized in a homozygous condition permits measuring their correlations with other more complex multiple factor characters, and thus furnishes an opportunity to determine to what extent they are correlated with the characters that differentiate maize from teosinte.

The hybrid between Tom Thumb pop corn and teosinte showed that the characters of maize were correlated only to a very slight degree and that in many cases there were definite disherences where characters derived, one from the maize and the other from the teosinte parent, tended to reappear together. With the numerous factors involved, largely in a heterozygous condition, only low correlations could be expected; but with simple or comparatively simple characters which can be recognized in the homozygous-recessive condition one would expect relatively higher, though fewer, correlations with the characters which differentiate maize from teosinte than were found in the Tom Thumb-teosinte hybrid.

CRINKLY × TEOSINTE

Crinkly is a variation of complex constitution affecting the form of leaf, the length of the leaf sheath, the stature of the plant, and the form of the terminal inflorescence. In hybrids with maize it has been found possible to separate this complex of characters into its several component parts. As stated by Emerson (*6*), "All of these characters are so variable, however, that some plants classed as crinkly do not show prominently one or other of them. Considering all leaf characters together with stature and form of tassel, it is usually easily possible to separate crinkly from normal plants, but occasionally the separation is somewhat difficult."

Typical plants of crinkly are of short stature and have compact tassels with relatively short branches and central spikes; the leaves are short and broad, usually folded and crinkled, and often with pronounced lobes at the base, while the sheaths are short and often fail to cover the nodes. In the hybrids with teosinte there also was a difference in color, the crinkly plants seemingly being of a much darker green than plants of normal teosinte. In extreme cases the upper leaves of crinkly plants fail to unroll; not unfrequently in these cases pistillate flowers develop in the tassel or, more rarely, an immature ear is produced in the place of the lowest tassel branch or in the axil of the uppermost leaf. The crinkly plant used as the female parent of the hybrid with teosinte represented an average expression of these characters and possessed none of the characteristics of extreme plants.

Two first-generation plants were grown in the greenhouse at Chula Vista, Calif., each producing several hundred seeds. Progenies from both of these F_1 plants were grown separately in the field, as well as a population of the first generation. The F_2 populations differed somewhat with respect to certain characters, thus precluding their combination in a statistical analysis without recourse to weighting factors; they therefore were analyzed separately.

With respect to the behavior of the crinkly character, the plants proved to be very much alike. The analysis of only one, therefore, is presented in detail.

An effort was made to get measurements of the various crinkly characters, such as length and width of leaf, stature, and dimensions of the various parts of the tassel, and, in addition, the plants were graded as to

the degree of crinkly leaves, degree of lobing, and degree of color, each on a scale of from 0 to 9. Aside from these grades, the plants were classified into normal and crinkly classes, with the result that 28.1 ± 2.1 per cent were adjudged to be crinklies. The fact that the second generation plants fell naturally into two groups representing 25 and 75 per cent of the individuals seems conclusive proof that a single gene is largely responsible for the differentiation. Unlike most monohybrid characters, however, there is no single morphological characteristic that is predominantly affected by this gene. At maturity the best pistillate inflorescence was harvested, and the various notes designed to measure the maize and teosinte characters were recorded.

CHARACTERS MEASURED

In the analysis of this hybrid 39 characters were studied, of which the means, standard deviations and probable errors are given in Table I for both the F_1 and F_2 populations, and the frequency distributions for the F_2 population are shown in figures 1 to 39.

DESCRIPTION OF CHARACTERS

1. HEIGHT.—The height of the main culm is measured from the surface of the ground to the tip of the central spike of the tassel, and the measurements are recorded in decimeters. The average height of teosinte is 23 decimeters, of crinkly maize, 12 decimeters, of ramose maize, 18 decimeters, of brachytic maize, 9 decimeters.

2. HEIGHT OF TALLEST SUCKER.—The height of the tallest sucker is obtained and recorded in the same manner as that of the main culm. In teosinte the tallest sucker is as high or higher than the central culm, while in the strains of maize used in these hybrids, suckers are produced but rarely, and they seldom are as tall as the main culm.

3. TOTAL SUCKER HEIGHT.—The total sucker height is the summation of the heights of all the branches arising at or below the surface of the ground, and is recorded in meters. The total sucker height in teosinte usually is 20, while in the strains of maize used in these hybrids the total sucker height seldom exceeds one meter.

4. NUMBER OF SUCKERS.—The number of suckers is the total number of branches arising at or below the surface of the ground. The number of suckers in teosinte is about 14, and in the strains of maize used in these hybrids the average number of suckers is less than 0.5.

5. LEAVES ABOVE.—Leaves above the uppermost branch of the main culm. This character corresponds to the number of nodes above the ear in maize. It is the number of leaves between the terminal inflorescence and the uppermost lateral branch. In teosinte this is 1; in crinkly, ramose, and brachytic maize 5 or 6.

6. TOTAL NUMBER OF LEAVES.—This character is the total number of leaves produced on the main culm from germination to maturity. About every fifth leaf is marked with small tags until the fifteenth, which is usually in good condition at maturity. Teosinte produces about 37 leaves, and the maize parents about 20.

7. LENGTH OF BRANCHING SPACE.—This is the length in cm. of the branched portion of the terminal inflorescence of the main culm. In teosinte this measurement is about 7 cm., in crinkly maize 15 cm., in ramose maize 28 cm., and in brachytic maize 12 cm.

8. LENGTH OF CENTRAL SPIKE.—The length in centimeters of the terminal spike of the staminate inflorescence of the main culm. In teosinte this measurement is about 8 cm., in crinkly maize 12 cm., in ramose maize 5 cm., and in brachytic maize 30 cm.

9. LENGTH OF LONGEST TASSEL BRANCH.—The length in centimeters of the longest branch of the terminal inflorescence of the main culm. In teosinte this measurement is about 10 cm., in crinkly maize 9 cm., in ramose maize 20 cm., and in brachytic maize 25 cm.

10. LENGTH OF GLUME.—Length of the outer glume in millimeters. The spikelet for this measurement was chosen from about the middle of the central spike. The glumes of teosinte are from 10 to 11 mm. in length; of crinkly maize 7 to 8 mm.

11. NUMBER OF TASSEL BRANCHES.—The number of branches, primary, secondary, tertiary, and upward, of the terminal staminate inflorescence of the main culm. In teosinte this is usually 23, in crinkly maize 17, in ramose maize 133, and in brachytic maize 36.

12. ROWS IN CENTRAL SPIKE.—The number of rows of alicoles on the central spike of the terminal inflorescence of the main culm. In teosinte there are invariably two rows of alicoles, while in maize the number is four or more.

13. LENGTH OF LEAF.—Length in decimeters of the longest leaf produced on the main culm. In teosinte this is about 12, in crinkly maize 5, in ramose and brachytic maize about 9.

14. WIDTH OF LEAF.—Width in centimeters of the longest leaf. The leaves of teosinte are between 6 and 7 cm. wide, of crinkly about 13 cm., of ramose and brachytic about 10 cm.

15. WIDTH INDEX.—The width of the longest leaf in centimeters divided by the length in decimeters and multiplied by 10. The leaves of teosinte are more than 10 times as long as broad, of crinkly about 3 times, and of ramose and brachytic 9 or 10 times.

16. LENGTH OF SHEATH.—Length in centimeters of the sheath of the longest leaf. The sheaths of teosinte are about three times as long as those of crinkly maize.

17. POSITION OF LONGEST LEAF.—The number of leaves above the longest leaf of the main culm. In teosinte there are about 15 leaves above the longest, in maize 8 or 9.

18. LEAVES ABOVE BEST INFLORESCENCE.—The number of leaves above the best inflorescence of the main culm. In these hybrids the entire branch is considered as the inflorescence. In maize this number would be the same as the "Leaves above," but in the second generation plants the uppermost inflorescence often is not the best, and in teosinte there usually are three leaves above the best branch.

19. LEAVES ON BEST INFLORESCENCE.—The number of leaves borne on the best inflorescence. The number of leaves forms a convenient way to count the number of nodes. The best branch of teosinte usually has 3 nodes, while the ear of maize is borne on a branch with 10 or more nodes.

20. LENGTH OF BEST INFLORESCENCE.—Length in centimeters of the best inflorescence produced on the main culm. The ear and ear stalk of maize are about one-fourth the length of the best branch of teosinte.

21. LENGTH OF EAR STALK OF BEST INFLORESCENCE.—The length in centimeters of the stalk of the best inflorescence. The length of the ear stalk of maize is about one-tenth that of the stalk of the best branch of teosinte.

22. LENGTH OF ♀ PORTION OF BEST INFLORESCENCE.—The length in centimeters of the pistillate portion of the terminal panicle of the best inflorescence. In teosinte this character would rarely exceed 5, while in the strain of maize used in these hybrids it would be about 20.

23. NUMBER OF BRANCHES ON BEST INFLORESCENCE.—The number of branches in the terminal panicle of the best lateral inflorescence of the main culm. In teosinte there would be from 3 to 10 such branches, in maize none.

24. ROWS IN TERMINAL SPIKE OF BEST INFLORESCENCE.—The number of rows of alicoles in the terminal spike of the best inflorescence. In teosinte there are 2, in the strains of maize used, 6 to 10.

25. POSITION OF BEST SPIKE.—The position of the best spike of the lateral inflorescence. If borne in the axil of the prophyllum of a lateral branch, the spike was recorded as 1, if borne as the terminal spike, as 2, if at some intermediate node as 3. In teosinte this would be 3, in maize 1. In the ramose hybrid these positions were recorded as 0, 1, and 2.

26. LENGTH OF BEST SPIKE.—Length in centimeters of the best single spike produced on the best lateral inflorescence of the main culm. In teosinte this length would be about 5 cm., in maize about 20.

27. NUMBER ROWS OF ALICOLES ON BEST SPIKE.—The number of rows of alicoles on the best spike. In teosinte the number of rows always would be 2, in maize 6 to 10.

28. NUMBER DOUBLE ♀ ALICOLES.—The number of double female alicoles on the best spike. In teosinte there would be no double female alicoles; in maize all would be of this type.

29. NUMBER SINGLE ♀ ALICOLES.—The number of single female alicoles on the above spike. In teosinte there would be from 5 to 10 such alicoles, in maize none.

30. NUMBER OF SPIKES IN PROPHYLLARY.—The number of spikes borne on the branch in the axil of the prophyllum of the best lateral branch of the main culm. In teosinte the number of spikes would be from 3 to 8; in the strains of maize used in these hybrids there would be no such branches.

31. DAYS TO POLLEN.—The number of days from planting until the first pollen was shed. The number of days would vary with the time of planting, late planting resulting in a shortened period. At the time these plantings were made teosinte required 184 days to anthesis, while the strains of maize used in these hybrids required 75 to 85 days.

32. DAYS TO SILK.—The number of days from planting until the first silks appeared. As with days to pollen, this period is influenced by the time of planting. In teosinte 178 days were required; in maize 80 to 90 days.

33. DAYS POLLEN TO SILK.—The number of days elapsing after the first pollen was shed until the first silks appeared. Teosinte is proterogynous (the silks appearing before the pollen is shed) while the crinkly form of maize is proterandrous (silks appearing after the anthesis). In the first generation of the crinkly hybrid the plants were proterandrous by a mean number of days of 2.08, while the second generation plants were proterogynous by a mean of 2.04 days; this is expressed in Table I as −2.04. Teosinte is proterogynous by an average of 6 days, while maize is proterandrous by from 2 to 6 days.

34. DEGREE OF CRINKLY.—An estimate of the degree of wrinkling of the leaf blades. The estimate was made on a scale of 0 to 9, smooth leaves being recorded as zero.

35. DEGREE OF LOBING.—An estimate of the degree of lobing of the leaves; no lobes being recorded as 0, and the highest degree of lobing as 9.

36. DEGREE OF COLOR.—An effort to grade the plants as to the color of the foliage, light green or teosinte color being recorded as 0, and extremely dark green as 9.

37. ALICOLE INDEX.—The number of single female alicoles divided by the sum of the single and double female alicoles and multiplied by 100. In teosinte this index would be 100, in maize 0.

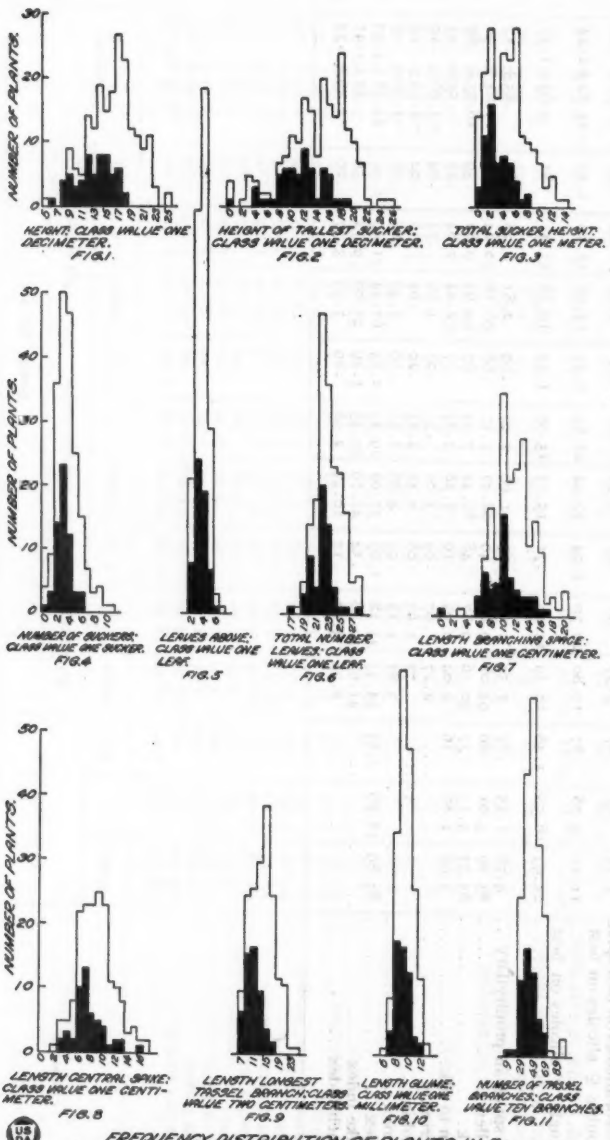
38. CENTRAL SPIKE INDEX.—The length of the central spike of the tassel divided by the total tassel length and multiplied by 100. This measurement is designed to show the relative length of the central spike. In maize it would be high, in teosinte low.

39. TASSEL BRANCH INDEX.—The length of the branching space of the tassel plus 10 minus the length of the longest tassel branch. This measurement is designed to show the relative length of the tassel branch. In maize this index would be high, in teosinte low.

TABLE I.—*Biometrical constants for the first and second generations of the crinkly × teosinte hybrid*

Characters.	First generation.			Second generation.									Difference.	Fig. number of frequency polygon.
				Entire population.			Crinkly group.			Normal group.				
	Mean.	σ	P. E.	Mean.	σ	P. E.	Mean.	σ	P. E.	Mean.	σ	P. E.		
Height	28.10	1.95	0.17	15.87	3.87	0.18	13.02	2.94	0.26	17.10	3.55	0.21	4.08±0.33	1
Height of tallest sucker	26.80	2.19	.19	13.94	5.01	.24	11.24	3.75	.34	15.08	5.06	.30	3.84± .46	2
Total sucker height	12.69	3.45	.30	4.66	3.15	.15	3.02	1.95	.18	5.29	3.28	.20	2.27± .26	3
Number of suckers	5.86	1.57	.14	3.81	1.90	.09	3.07	1.20	.11	4.08	2.80	.17	1.01± .20	4
Leaves above	3.22	.64	.06	3.68	.97	.05	3.47	.93	.08	3.77	.96	.06	.30± .10	5
Total number of leaves	24.03	1.24	.11	23.06	2.08	.11	21.98	1.77	.16	23.50	2.08	.12	1.52± .17	6
Length of branching space	19.12	1.75	.16	11.67	2.94	.14	10.12	2.92	.26	12.32	2.96	.18	2.20± .32	7
Length of central spike	12.44	2.19	.20	8.73	2.97	.15	7.63	2.57	.23	9.14	2.96	.18	1.51± .28	8
Length of longest tassel branch	20.02	2.86	.26	13.16	3.74	.18	10.05	2.38	.21	14.45	3.48	.21	4.40± .28	9
Length of glume	10.68	1.33	.12	9.47	1.36	.07	8.98	1.16	.10	9.65	1.32	.08	.67± .14	10
Number of tassel branches	60.80	7.41	.67	43.17	13.60	.64	37.78	12.40	1.12	45.36	13.50	.80	7.58±1.37	11
Rows in central spike	4.00	.00	.00	3.89	.73	.04	4.24	.47	.04	3.77	.72	.04	−.47± .00	12
Length of leaf	10.00	.87	.08	6.84	1.27	.06	5.54	.89	.08	7.40	.94	.05	1.86± .10	13
Width of leaf	8.98	.12	.11	7.79	1.78	.09	9.07	1.94	.18	7.27	1.35	.08	−1.80± .20	14
Width index	8.98	1.66	.15	11.96	4.47	.21	16.76	4.68	.42	9.94	1.84	.10	−6.82± .44	15
Length of sheath	18.36	2.18	.19	13.27	2.89	.14	10.25	1.73	.16	14.54	2.28	.13	4.29± .20	16
Position of longest leaf	9.33	1.02	.90	7.88	1.58	.08	7.47	1.27	.11	8.06	1.65	.10	.59± .14	17
Leaves above best inflorescence	5.26	.67	.06	4.72	1.00	.05	4.40	1.02	.09	4.86	.92	.05	.46± .10	18
Leaves on best inflorescence	5.59	.82	.07	5.56	1.29	.06	5.44	1.23	.11	5.60	1.32	.08	.16± .14	19
Length of best inflorescence	57.33	18.22	1.62	19.85	8.36	.41	15.09	3.77	.34	21.88	9.01	.53	6.79± .63	20
Length of ear stalk of best inflorescence	42.71	15.97	1.41	11.37	13.89	.39	7.44	3.64	.33	13.02	8.74	.52	5.58± .61	21
Length of ♀ portion of best inflorescence	1.07	1.80	.16	6.12	2.93	.14	6.84	1.95	.18	5.96	2.96	.18	−.88± .24	22
Number of branches on best inflorescence	10.50	3.32	.30	2.02	3.14	.16	1.09	2.26	.20	2.42	3.37	.20	1.33± .28	23

Rows in terminal spike of best inflorescence	3.97	.00	.00	3.57	.78	.04	3.66	.69	.06	3.53	.81	.49	−.13± .49	24
Position of best spike	1.07	.36	.36	1.42	.63	.63	1.49	.62	.06	1.39	.64	.38	−.10± .37	25
Length of best spike	9.47	1.40	.13	8.02	1.58	.08	7.84	1.48	.13	8.11	1.61	.10	.27± .17	26
Number rows of alicoles on best spike	3.35	.83	.07	3.39	.97	.05	3.53	−.76	.07	3.32	.95	.57	−.21± .56	29
Number double ♀ alicoles on best spike	11.21	9.78	.87	19.80	20.70	1.04	30.44	21.65	1.95	15.62	18.60	1.12	−14.82±2.24	27
Number single ♀ alicoles on best spike	24.93	16.58	1.48	18.59	14.10	.71	15.23	15.05	1.35	19.88	13.45	.81	4.65±1.57	28
Number of spikes in prophyllary	4.76	1.35	.12	2.54	1.52	.07	1.96	1.01	.09	2.81	2.38	.14	.85± .17	30
Days to pollen	83.29	3.01	.26	94.01	9.65	.49	88.52	7.57	.68	96.16	10.04	.60	17.64± .90	31
Days to silk	85.37	4.15	.37	92.36	9.87	.48	86.41	7.44	.67	94.64	9.82	.59	18.23± .89	32
Days pollen to silk	2.08	1.86	.16	−2.04	2.03	.10	−2.28	3.04	.27	−2.24	2.84	.17	.03± .32	33
Degree of crinkly	.....	.....	.....	2.27	.87	.04	3.02	.73	.07	1.96	.73	.04	−1.06± .10	34
Degree of lobing	.....	.....	.....	.72	1.63	.08	2.41	2.25	.20	.05	.38	.02	−2.36± .20	35
Degree of color	.....	.....	.....	3.81	1.15	.05	4.86	1.14	.10	3.40	.86	.05	−1.46± .10	36
Alicole index	63.89	28.26	2.53	54.43	33.18	1.67	37.02	29.23	2.63	61.34	31.99	1.92	24.32±3.30	37
Central spike index	.....	.....	.....	41.93	10.48	.54	41.70	12.45	1.29	42.00	9.74	.58	.30±1.41	38
Tassel branch index	.....	.....	.....	8.58	3.45	.17	10.44	2.98	.29	7.95	3.37	.20	−2.49± .35	39



FREQUENCY DISTRIBUTION OF PLANTS IN F_2
SHADED PORTION REPRESENTS PLANTS CLASSED AS CRINKLY.

FIGURES 1 TO 11

FIG. 1.—Height; frequency distribution of plants in F_3. Class value, 1 decimeter. Shaded portion represents plants classed as crinkly.

FIG. 2.—Height of tallest sucker; frequency distribution of plant in F_2. Class value, 1 decimeter. Shaded portion represents plants classed as crinkly.

FIG. 3.—Total sucker height; frequency distribution of plants in F_2. Class value, 1 meter. Shaded portion represents plants classed as crinkly.

FIG. 4.—Number of suckers; frequency distribution of plants in F_2. Class value, 1 sucker. Shaded portion represents plants classed as crinkly.

FIG. 5.—Leaves above; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as crinkly.

FIG. 6.—Total number of leaves; frequency distribution of plants in F_2. Class value one leaf. Shaded portion represents plants classed as crinkly.

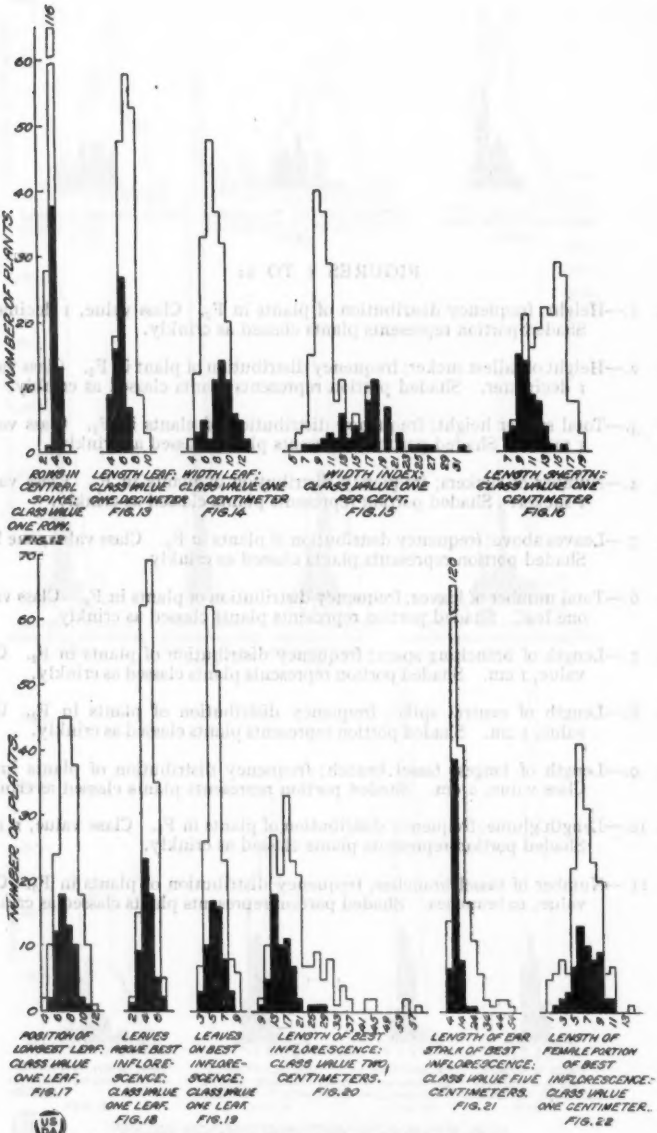
FIG. 7.—Length of branching space; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as crinkly.

FIG. 8.—Length of central spike; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as crinkly.

FIG. 9.—Length of longest tassel branch; frequency distribution of plants in F_2. Class value, 2 cm. Shaded portion represents plants classed as crinkly.

FIG. 10.—Length glume; frequency distribution of plants in F_2. Class value, 1 mm. Shaded portion represents plants classed as crinkly.

FIG. 11.—Number of tassel branches; frequency distribution of plants in F_2. Class value, 10 branches. Shaded portion represents plants classed as crinkly.


NUMBER OF PLANTS
ROWS IN CENTRAL SPIKE; CLASS VALUE ONE ROW. FIG. 12
LENGTH LEAF; CLASS VALUE ONE DECIMETER FIG. 13
WIDTH LEAF; CLASS VALUE ONE CENTIMETER FIG. 14
WIDTH INDEX; CLASS VALUE ONE PER CENT. FIG. 15
LENGTH SHEATH; CLASS VALUE ONE CENTIMETER FIG. 16
POSITION OF LOWEST LEAF; CLASS VALUE ONE LEAF. FIG. 17
LEAVES ABOVE BEST INFLORESCENCE; CLASS VALUE ONE LEAF. FIG. 18
LEAVES ON BEST INFLORESCENCE; CLASS VALUE ONE LEAF. FIG. 19
LENGTH OF BEST INFLORESCENCE; CLASS VALUE TWO CENTIMETERS. FIG. 20
LENGTH OF EAR STALK OF BEST INFLORESCENCE; CLASS VALUE FIVE CENTIMETERS. FIG. 21
LENGTH OF FEMALE PORTION OF BEST INFLORESCENCE; CLASS VALUE ONE CENTIMETER. FIG. 22

FREQUENCY DISTRIBUTION OF PLANTS IN F_2.
SHADED PORTION REPRESENTS PLANTS CLASSED AS CRINKLY.

FIGURES 12 TO 22

FIG. 12.—Rows in central spike; frequency distribution of plants in F_2. Class value one row. Shaded portion represents plants classed as crinkly.

FIG. 13.—Length of leaf; frequency distribution of plants in F_2. Class value, 1 decimeter. Shaded portion represents plants classed as crinkly.

FIG. 14.—Width of leaf; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as crinkly.

FIG. 15.—Width index; frequency distribution of plants in F_2. Class value, 1 per cent. Shaded portion represents plants classed as crinkly.

FIG. 16.—Length of sheath; frequency distribution of plants in F_2. Class value, 1 centimeter. Shaded portion represents plants classed as crinkly.

FIG. 17.—Position of longest leaf; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as crinkly.

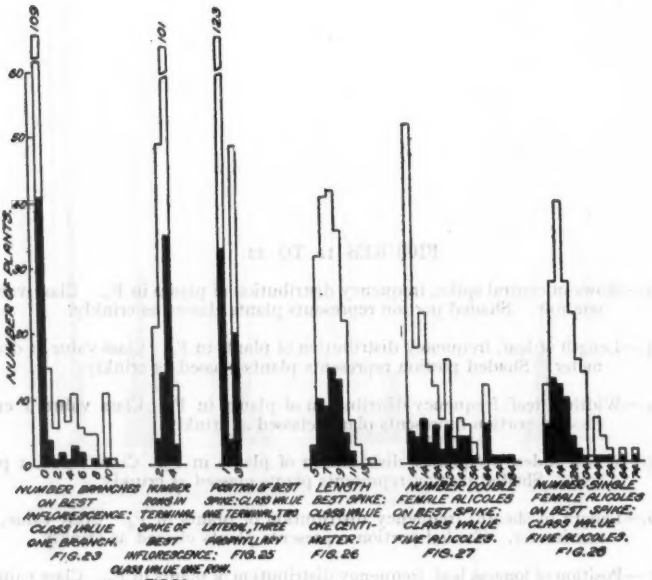
FIG. 18.—Leaves above best inflorescence; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as crinkly.

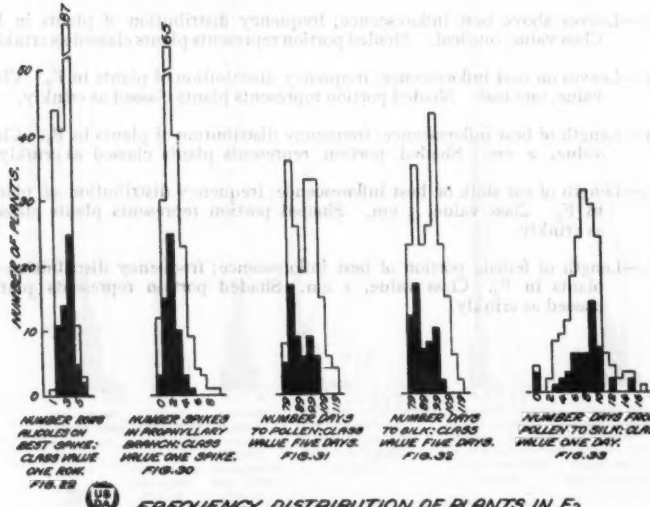
FIG. 19.—Leaves on best inflorescence; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as crinkly.

FIG. 20.—Length of best inflorescence; frequency distribution of plants in F_2. Class value, 2 cm. Shaded portion represents plants classed as crinkly.

FIG. 21.—Length of ear stalk of best inflorescence; frequency distribution of plants in F_2. Class value, 5 cm. Shaded portion represents plants classed as crinkly.

FIG. 22.—Length of female portion of best inflorescence; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as crinkly.


NUMBER OF PLANTS.
109
101
123
NUMBER BRANCHES ON BEST INFLORESCENCE: CLASS VALUE ONE BRANCH. FIG. 23
NUMBER ROWS IN TERMINAL SPIKE OF BEST INFLORESCENCE: CLASS VALUE ONE ROW. FIG. 24
POSITION OF BEST SPIKE: CLASS VALUE ONE TERMINAL, TWO LATERAL, THREE PROPHYLLARY FIG. 25
LENGTH BEST SPIKE: CLASS VALUE ONE CENTIMETER. FIG. 26
NUMBER DOUBLE FEMALE ALICOLES ON BEST SPIKE: CLASS VALUE FIVE ALICOLES. FIG. 27
NUMBER SINGLE FEMALE ALICOLES ON BEST SPIKE: CLASS VALUE FIVE ALICOLES. FIG. 28


NUMBER OF PLANTS.
97
65
NUMBER ROWS ALICOLES ON BEST SPIKE: CLASS VALUE ONE ROW. FIG. 29
NUMBER SPIKES IN PROPHYLLARY BRANCH: CLASS VALUE ONE SPIKE. FIG. 30
NUMBER DAYS TO POLLEN: CLASS VALUE FIVE DAYS. FIG. 31
NUMBER DAYS TO SILK: CLASS VALUE FIVE DAYS. FIG. 32
NUMBER DAYS FROM POLLEN TO SILK: CLASS VALUE ONE DAY. FIG. 33

FREQUENCY DISTRIBUTION OF PLANTS IN F_2.
SHADED PORTION REPRESENTS PLANTS CLASSED AS CRINKLY.

FIGURES 23 TO 33

FIG. 23.—Number of branches on best inflorescence; frequency distribution of plants in F_2. Class value, one branch. Shaded portion represents plants classed as crinkly.

FIG. 24.—Number of rows in terminal spike of best inflorescence; frequency distribution of plants in F_2. Class value, one row. Shaded portion represents plants classed as crinkly.

FIG. 25.—Position of best spike; frequency distribution of plants in F_2. Class value, one terminal, two lateral, three prophyllary. Shaded portion represents plants classed as crinkly.

FIG. 26.—Length of best spike; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as crinkly.

FIG. 27.—Number of double female alicoles on best spike; frequency distribution of plants of F_2. Class value, five alicoles. Shaded portion represents plants classed as crinkly.

FIG. 28.—Number of single female alicoles on best spike; frequency distribution of plants of F_2. Class value, five alicoles. Shaded portion represents plants classed as crinkly.

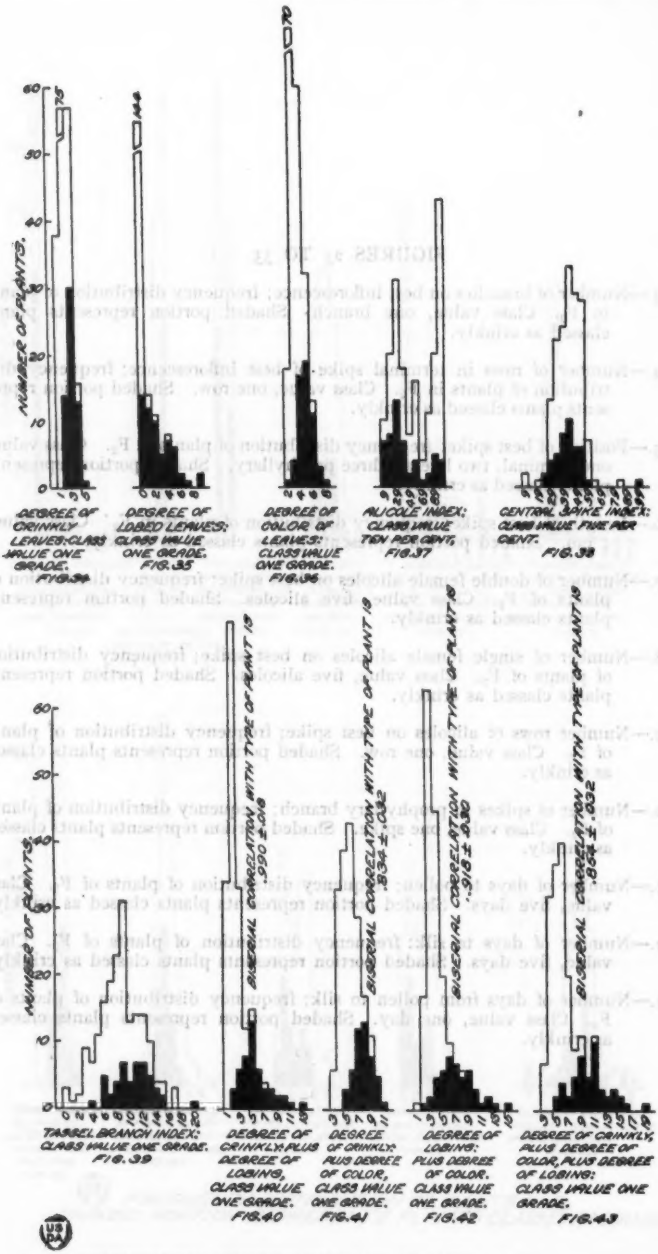
FIG. 29.—Number rows of alicoles on best spike; frequency distribution of plants of F_2. Class value, one row. Shaded portion represents plants classed as crinkly.

FIG. 30.—Number of spikes in prophyllary branch; frequency distribution of plants of F_2. Class value, one spike. Shaded portion represents plants classed as crinkly.

FIG. 31.—Number of days to pollen; frequency distribution of plants of F_2. Class value, five days. Shaded portion represents plants classed as crinkly.

FIG. 32.—Number of days to silk: frequency distribution of plants of F_2. Class value, five days. Shaded portion represents plants classed as crinkly.

FIG. 33.—Number of days from pollen to silk; frequency distribution of plants of F_2. Class value, one day. Shaded portion represents plants classed as crinkly.


NUMBER OF PLANTS.
DEGREE OF CRINKLY LEAVES: CLASS VALUE ONE GRADE. F1G.34
DEGREE OF LOBED LEAVES: CLASS VALUE ONE GRADE. F1G.35
DEGREE OF COLOR OF LEAVES: CLASS VALUE ONE GRADE. F1G.36
ALCOLE INDEX: CLASS VALUE TEN PER CENT. F1G.37
CENTRAL SAINE INDEX: CLASS VALUE FIVE PER CENT. F1G.38
TASSEL BRANCH INDEX: CLASS VALUE ONE GRADE. F1G.39
DEGREE OF CRINKLY; PLUS DEGREE OF LOBING, CLASS VALUE ONE GRADE. F1G.40
DEGREE OF CRINKLY; PLUS DEGREE OF COLOR, CLASS VALUE ONE GRADE. F1G.41
DEGREE OF LOBING; PLUS DEGREE OF COLOR. CLASS VALUE ONE GRADE. F1G.42
DEGREE OF CRINKLY, PLUS DEGREE OF COLOR, PLUS DEGREE OF LOBING; CLASS VALUE ONE GRADE. F1G.43
BISERIAL CORRELATION WITH TYPE OF PLANT IS .950 ± .010
BISERIAL CORRELATION WITH TYPE OF PLANT IS .834 ± .032
BISERIAL CORRELATION WITH TYPE OF PLANT IS .918 ± .030
BISERIAL CORRELATION WITH TYPE OF PLANT IS .884 ± .022

FREQUENCY DISTRIBUTION OF PLANTS IN F_2.
SHADED PORTION REPRESENTS PLANTS CLASSED AS CRINKLY.

FIGURES 34 TO 43

FIG. 34.—Degree of crinkly leaves; frequency distribution of plants of F_2. Class value, one grade. Shaded portion represents plants classed as crinkly.

FIG. 35.—Degree of lobed leaves; frequency distribution of plants of F_2. Class value, one grade. Shaded portion represents plants classed as crinkly.

FIG. 36.—Degree of color of leaves; frequency distribution of plants of F_2. Class value, one grade. Shaded portion represents plants classed as crinkly.

FIG. 37.—Alicole index; frequency distribution of plants of F_2. Class value, 10 per cent. Shaded portion represents plants classed as crinkly.

FIG. 38.—Central spike index; frequency distribution of plants of F_2. Class value, 5 per cent. Shaded portion represents plants classed as crinkly.

FIG. 39.—Tassel branch index; frequency distribution of plants of F_2. Class value, one grade. Shaded portion represents plants classed as crinkly.

FIG. 40.—Degree of crinkly plus degree of lobing; frequency distribution of plants in F_2. Class value, one grade. Biserial correlation with type of plant is 0.990 ± 0.018. Shaded portion represents plants classed as crinkly.

FIG. 41.—Degree of crinkly plus degree of color; frequency distribution of plants in F_2. Class value, one grade. Biserial correlation with type of plant is 0.834 ± 0.032. Shaded portion represents plants classed as crinkly.

FIG. 42.—Degree of lobing plus degree of color; frequency distribution of plants in F_2. Class value, one grade. Biserial correlation with type of plant is 0.918 ± 0.030. Shaded portion represents plants classed as crinkly.

FIG. 43.—Degree of crinkly plus degree of color plus degree of lobing; distribution of plants in F_2. Class value, one grade. Biserial correlation with type of plant is 0.854 ± 0.032. Shaded portion represents plants classed as crinkly.

74027—24——3

INHERITANCE OF MEASURED CHARACTERS

Although plant height is one of the distinguishing characteristics of crinkly, none of the measurements of height in the second generation showed indications of Mendelian segregation, the distributions being similar to those of the same character in the Tom Thumb-Florida cross (*5*). The same is true also of the number of suckers, of which Euchlaena has a great many and crinkly none. It is of interest to note that the mean number of suckers in the crinkly hybrid was only about one-fourth the mean number produced in the Tom Thumb hybrid.

In the number of leaves above the uppermost lateral inflorescence both F_1 and F_2 differed from previous hybrids of maize and teosinte. The mean of 3.22 ± 0.06 nodes above the uppermost lateral inflorescence on the F_1 plants is much greater than is usually the case, and is of particular interest, in view of the rather definite tendency of the crinkly variation to produce an ear in the axil of the uppermost leaf.

In the second generation the mean number was only slightly increased, resembling other hybrids in that the mean of the second-generation plants with respect to this character closely approximates that of the F_1. In range some plants were produced with more nodes above the uppermost lateral inflorescence than would be found in the maize parent, while none returned completely to the teosinte parent in this character.

In the total number of leaves produced on the main stalk, the inheritance was as expected and the distribution is regular. This applies also to the characters of the staminate inflorescence, though it is worthy of note that the number of tassel branches is very large, both in the first and second generation. In fact, the number of tassel branches in the first generation of the crinkly hybrid was greatly in excess of the number found in the F_1 of the ramose hybrid, to be discussed, the positions being reversed in the second generations of these hybrids.

The number of days from germination to flowering and the alicole index are the only characters of the 38 which show indication of Mendelian or discontinuous inheritance, the distribution of the plants for these characters (fig. 31, 32, and 37) being bimodal. The bimodality of the distributions for the number of days to flowering are of particular interest, since crosses between early and late varieties of maize have never shown any indication of bimodality in the F_2. The alicole index showed a bimodal distribution in the second generation of the Tom Thumb-teosinte hybrid also, but while the greatest number of plants are found with a high index in the crinkly hybrid, the reverse is true for the Tom Thumb hybrid. This behavior follows from that of the F_1, where it was found that in the crinkly hybrid the single female alicole form of teosinte was partially dominant to the double female alicole of maize. The general character of the spikes, however, resembled the F_1 of teosinte $\times$ Tom Thumb in that they were flat and broad, suggesting a secondary ear of maize much more nearly than a spike of teosinte.

The inheritance of the proterogynous habit of teosinte, as expressed by the number of days from pollen to silk, was very different in the crinkly hybrid from previous maize teosinte hybrids, in that though the F_1 was proterandrous by a mean of 2.08 days the F_2 was proterogynous by an almost equal time, i. e., 2.04 days. In other hybrids the decidedly proterogynous habit of teosinte has failed to reappear in the F_2, while the F_1 usually is even more proterandrous than the maize parent.

The proterogynous habit is one which may be influenced greatly by photoperiodism or other environmental factors. Many varieties of maize from South America, indigenous near the equator, are so decidedly proterandrous when grown in the United States as to interfere seriously with the production of seed.

Euchlaena seems to be proterogynous, regardless of the flowering date, and even when hastened into flower by artificially shortening the day.

Even in maize, though the plant as a whole usually is proterandrous, the individual inflorescences seem to be inherently proterogynous. If conditions force pistillate flowers to develop in an inflorescence normally staminate, the resulting flowers always are proterogynous. When gyandrous inflorescences are normal to the strain, as in tassel seed, they also are always proterogynous, while in the andromonoecious dwarf variation the full development of the anthers occurs after the silks have appeared.

None of the characters of the crinkly variations showed discontinuous inheritance, though most of the crinkly characteristics were recovered in the F_2 in an even more extreme form than was found in the parental progeny. Crinkly and teosintelike plants from the F_2, together with their inflorescences, are shown in Plates 2, 3, 4, and 5.

Notwithstanding the failure to obtain bimodal distributions of these characters, the frequency polygons in figures 1, 7, 8, 9, 11, 13, 14, 15, 16, 34, 35, 36, 37, and 39, all clearly show the high degree of development, in the plants empirically classed as crinkly, of the characters commonly associated in this variation.

These relationships are measured by the coefficients of biserial correlations presented in Tables IV and V.

CORRELATIONS BETWEEN CHARACTERS

This brings us to the consideration of the whole problem of character relationships. Two questions may be answered by the data at hand: First, to what extent the character complex comprising the crinkly variation tends to remain associated; second, to what extent all or any of these characters are associated with other maize characters not involved in the crinkly variation.

Difficulties are encountered at the start in the proper interpretation of the correlation coefficients, since by direct means it is not possible to distinguish purely physiological relationships from those which are genetic.

Recourse may be had to the method suggested by Collins of comparing the degree of correlation in the F_1 with that found in the F_2 (*2*). Correlations in the F_1 are held to be due to physiological relationships, while any differences between F_1 and F_2 correlations may be ascribed to genetic causes. The coefficients of correlation between all the characters studied in this hybrid are given in Table II.

TABLE II.—*Coefficients of correlation among the characters of the plants of the first and second generations of the hybrid between crinkly maize and Florida teosinte* [a]

Character.	Height.		Height of tallest sucker.		Total sucker height.		Number of suckers.		Leaves above.		Total number of leaves.		Length of branching space.		Length of central spike.		Length of longest tassel branch.		Length of glume.	
	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1
Height			.716	.714	.631	.371	.228	−.032	D .214	.002	.340	.458	D .570	.145	D .335	.119	.618	.055	.352	.155
Height of tallest sucker	.716	.714			.890	.478	.443	.114	D .041	.063	.229	.416	D .411	.078	D .198	.187	.484	−.055	.218	.158
Total sucker height	.631	.371	.890	.478			.332	.499	— 094	.045	.216	.263	.319	−.149	D .203	.089	.435	.152	.222	−.077
Number of suckers	.228	−.032	.443	.114	.332	.499			−.031	−.063	.028	−.110	.074	−.265	D .191	−.152	.259	.190	.117	−.055
Leaves above	D .214	.002	D .041	.063	−.094	.045	−.031	−.063			D .062	.243	D .217	−.138	.255	−.045	D .229	−.168	D .060	−.173
Total number of leaves	.340	.458	.229	.416	.216	.263	.028	−.110	D .062	.243			.049	−.045	−.125	.345	D −.045	−.077	D −.064	.055
Length of branching space	.570	.145	D .411	.078	.319	−.149	.074	−.265	D .217	−.138	.049	−.045			D .195	−.032	.549	.114	.245	.119
Length of central spike	D .335	.119	D .198	.187	D .203	.089	D .191	−.152	.255	−.045	−.125	.345	D .195	−.032			D .622	.063	D .454	.274
Length of longest tassel branch	.618	.055	.484	−.055	.435	.152	.259	.190	D .229	−.168	D −.045	−.077	.549	.114	D .622	.063			.459	.003
Length of glume	.352	.155	.218	.158	.222	−.077	.117	−.055	D .060	−.173	D −.064	.055	.245	.119	D .454	.274	.459	.003		
Number of tassel branches	.464	− 089	.442	−.138	.287	−.032	.030	.173	D .071	−.004	.312	−.263	.542	−.055	D .126	−.323	.361	.247	D −.013	−.055
Rows in central spike	−.169		−.194		−.157		−.116		D −.031		−.098		−.059		D −.020		−.273		−.022	
Length of leaf	.698	.441	.490	.439	.438	.100	.141	−.003	D .208	−.190	.487	.193	.480	−.257	D .205	.134	.530	−.105	.251	.321
Width of leaf	−.041	−.123	D .092	−.017	−.125	.195	−.128	.435	D −.010	.063	−.162	−.350	−.040	−.030	.014	−.440	−.130	.171	−.091	−.336
Width index	−.434	−.327	−.233	−.247	−.354	.083	−.177	.313	D −.132	.149	−.374	−.372	−.320	−.149	D −.127	−.378	−.417	.171	−.209	−.404
Length of sheath	.598	.228	.405	.055	.333	−.200	.145	−.077	D .180	.297	.326	−.020	.391	.171	D .373	.187	.531	.119	.307	.226
Position of longest leaf	.222	.210	.120	.131	.088	−.010	.010	−.145	D .063	.145	.771	.470	.020	−.100	−.166	.063	D −.120	−.145	D −.138	.007
Leaves above best inflorescence	D .219	.045	D .089	−.032	D .031	.110	−.020	.030	D .524	.249	D .341	.219	D .020	.045	−.028	−.045	D .064	.100	D .041	−.045
Leaves on best inflorescence	D .126	.045	D .223	−.032	D .152	−.026	D .034	−.105	.165	−.055	D .000	.070	D .244	.198	D −.020	−.063	D .119	.187	D .014	.095
Length of best inflorescence	.464	.526	.465	.350	.195	.332	.323	−.084	D .044	.071	D −.010	.499	.358	.100	D .226	.305	.402	.245	.178	.283
Length ear stalk, best infl	.365	.503	.409	.355	.660	.330	.374	−.084	D −.026	.063	D −.000	.544	.275	.110	D .163	.320	.313	.247	.126	.260
Length ♀ portion, best infl	−.014	−.318	−.139	−.208	−.330	−.231	−.241	−.045	.310	−.004	−.064	−.233	D .122	−.045	.166	.089	−.024	−.303	D .048	−.045
Branches on best infl	.248	.352	.272	.185	.367	.089	.159	.070	D .041	−.089	.092	.351	.291	.171	D −.000	.230	.173	.237	.055	.145
Rows terminal spike, best infl	D .050	.408	D .109	.237	D .045	.182	−.010	−.145	.223	.071	−.081	.173	.127	.134	.216	−.100	.000	−.077	D .151	.028
Position of best spike	D −.075	.349	D −.186	.247	D −.106	.233	D −.046	−.084	D .030	−.077	D −.218	.193	.017	−.077	D .066	.100	.098	.077	.049	−.027
Length of best spike	D .344	−.435	D .207	−.348	D −.180	.165	−.253	.089	.306	−.017	D .093	−.247	.224	−.017	.244	−.145	.207	.158	.061	−.155
Rows of alicoles on best spike	D .057	−.032	D .056	−.162	D .000	.179	−.000	.022	.220	−.045	−.085	−.084	D .238	.063	.169	.032	D .026	−.134	−.028	.084
Double ♀ alicoles on best spike	D .037	−.251	−.123	−.063	−.261	−.231	−.289	.010	.169	.089	−.191	−.198	D .067	.077	.039	−.105	−.091	.095	−.082	−.063
Single ♀ alicoles on best spike	.169	−.014	.114	−.127	.476	.071	.123	−.010	D .044	−.010	.033	−.014	.206	−.045	D .243	.071	.183	−.006	.091	.123
Spikes in prophyllary	.280	.267	.318	.279	.380	.193	.259	.055	−.116	.100	.048	.458	.068	−.084	−.010	.305	.207	.123	.036	.142
Days to pollen	.155	.257	.149	.300	.067	.145	D −.083	.292	−.206	.138	.536	.573	D −.052	.182	−.206	.420	D −.000	.017	D −.068	.063
Days to silk	.200	.335	.174	.369	.032	.176	D −.128	.329	−.176	.032	.544	.607	.043	.185	−.160	.505	.066	.055	D −.094	.105
Days pollen to silk	D .131	.327	D .065	.330	−.115	.158	−.125	.257	.124	−.142	−.046	.416	D .313	.114	.172	.439	D .225	.095	D −.059	.131
Degree of crinkly	−.177		−.061		−.150		−.143		D −.027		−.131		−.078		D −.131		−.267		−.184	
Degree of lobing	−.256		−.239		−.204		−.235		D − 042		−.086		−.186		D −.157		−.447		−.080	
Degree of color	−.249		−.140		−.073		D .014		D −.061		−.217		−.137		.000		−.238		−.044	
Alicole index	.755	.134	.460	−.071	.572	.127	.519	−.006	−.066	−.045	.060	.045	.229	.020	D .134	.105	.282	−.045	.140	.077
Type of plant	−.628		−.458		−.444		−.334		D −.181		−.445		−.452		D −.316		−.711		−.300	

Character.	Number of tassel branches.		Rows in central spike.		Length of leaf.		Width of leaf.		Width index.		Length of sheath.		Position of longest leaf.		Leaves above best inflorescence.		Leaves on best inflorescence.		Length of best inflorescence.	
	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1
Height	.464	−.089	−.169	.....	.698	.441	−.041	−.123	−.434	−.327	.598	.228	.222	.210	D .219	.045	D .126	.045	.464	.526
Height of tallest sucker	.442	−.138	−.194	.....	.490	.439	D .092	−.017	−.233	−.247	.405	.055	.120	.131	D .089	−.032	D .223	−.032	.465	.350
Total sucker height	.287	−.032	−.157	.....	.438	.100	−.125	.195	−.354	.083	.333	−.200	.088	−.010	D .031	.110	D .152	−.026	.195	.332
Number of suckers	.030	.173	−.116	.....	.141	−.003	−.128	.435	−.177	.313	.145	−.077	.010	−.145	−.020	.030	D .034	−.105	.323	−.084
Leaves above	D .071	−.004	D −.031	.....	D .208	−.190	D −.010	.063	D −.132	.149	D .180	.297	D .063	.145	.524	.249	.165	−.055	D .044	.071
Total number of leaves	.312	−.263	−.098	.....	.487	.193	−.162	−.350	−.374	−.372	.316	−.020	.771	.470	D .341	.219	D .000	.070	D −.010	.499
Length of branching space	.542	−.055	−.059	.....	.480	.257	−.040	−.030	−.320	−.149	.391	.171	.020	−.100	D .020	.045	D .244	.198	.358	.100
Length of central spike	D .126	−.323	D −.020	.....	D .205	.134	.014	−.440	D −.127	−.378	D .373	.187	−.166	.063	.028	−.045	D −.020	−.063	D .226	.305
Length of longest tassel branch	.361	.247	−.273	.....	.530	−.105	−.130	.171	−.417	.171	.531	.119	D −.120	−.145	D .064	.100	D .119	.187	.402	.245
Length of glume	D −.013	−.055	−.022	.....	.251	.321	−.091	−.336	−.209	−.404	.307	.226	D −.138	.007	D .041	−.045	D .014	.095	.178	.283
Number of tassel branches	.....	.....	D .092	.....	.438	.073	D .130	.245	−.172	.138	.330	.164	.289	.032	D .080	−.017	D .296	.084	.284	−.157
Rows in central spike	D .092	.....	.....	.....	−.205	.....	.205	.....	.259	.....	−.189	.....	−.014	.....	D −.169	.....	.014	.....	−.094	.....
Length of leaf	.438	.073	−.205	.....	.....	.....	−.251	−.235	−.746	−.691	.671	.530	.370	.253	D .215	−.014	D .045	.105	.347	.312
Width of leaf	D .130	.245	.205	.....	−.251	−.235	.....	.....	.788	.860	−.388	−.342	−.195	−.403	D −.124	.100	.127	.017	−.086	−.266
Width index	−.172	.138	.259	.....	−.746	−.691	.788	.860	.....	.....	−.646	−.542	−.323	−.429	D .210	.084	.041	−.032	−.262	−.366
Length of sheath	.330	.164	−.189	.....	.671	.530	−.388	−.342	−.646	−.542	.....	.....	.349	.466	D .150	.045	D .028	.179	.318	.032
Position of longest leaf	.289	.032	−.014	.....	.370	.253	−.195	−.403	−.323	−.429	.349	.466	.....	.....	D .355	.165	−.017	.100	D −.047	.131
Leaves above best inflorescence	D .080	−.017	D −.169	.....	.215	−.014	D −.124	.100	D −.210	.084	D .150	.045	D .355	.165	.....	.....	.189	.518	D .187	.045
Leaves on best inflorescence	D .296	.084	.014	.....	.045	.105	.127	.017	.041	−.032	D .028	.179	−.017	.100	.189	.518	.....	.....	D .260	.045
Length of best inflorescence	.284	−.157	−.094	.....	.347	.312	−.086	−.366	−.262	−.366	.318	.032	D −.047	.131	D .187	.045	D .260	.045	.....	.....
Length ear stalk, best infl	.227	−.165	−.069	.....	.285	.313	−.120	−.230	−.250	−.338	.246	−.008	D −.022	.089	D .174	.063	D .236	.084	.961	.973
Length ♀ portion, best infl	−.096	.185	.115	.....	−.066	.142	.118	−.145	.102	−.170	−.022	.055	−.069	−.008	.092	−.095	.111	−.182	−.350	−.359
Branches on best infl	.418	− 025	D .076	.....	.269	.255	−.026	−.198	−.183	−.290	.205	.252	.128	.134	D .082	−.017	D .101	.045	.492	.624
Rows terminal spike, best infl	D .090	−.063	.214	.....	.000	.105	.240	.152	.166	.055	D .020	−.114	.....	.....	D −.056	.247	.182	.152	D .075	.077
Position of best spike	D −.141	.020	−.050	.....	D −.066	.203	−.125	−.032	−.054	−.138	D −.028	.321	.....	.....	D .017	.155	D .063	.247	.125	−.239
Length of best spike	D .157	.084	.035	.....	D .180	−.055	.262	−.055	.079	.007	D .161	−.030	.....	.....	.173	.251	.129	.219	D .010	.285
Rows of alicoles on best spike	D .089	−.071	.277	.....	−.040	.110	.137	−.110	.121	−.142	D .063	.119	.....	.....	D −.046	−.142	.197	.063	−.048	.235
Double ♀ alicoles on best spike	−.020	.045	.032	.....	−.165	−.272	.269	.190	.287	.292	−.208	−.224	.....	.....	.014	.045	.177	.105	−.069	−.347
Single ♀ alicoles on best spike	.069	.142	D .131	.....	.098	.300	D .033	.237	−.049	.340	.178	.272	.....	.....	−.075	.027	D .100	.077	.020	.287
Spikes on prophyllary	.037	−.084	−.122	.....	.177	.030	−.094	−.155	−.141	−.134	.075	.105	.....	.....	−.028	.095	D .014	−.212	.324	.195
Days to pollen	.171	−.155	−.105	.....	.302	.055	−.355	−.354	−.425	−.294	.207	.114	.....	.....	D .127	.217	−.190	.123	.014	.168
Days to silk	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Days pollen to silk	D .308	−.005	.114	.....	D .032	.138	.151	−.226	.095	−.243	D .138	.182	.....	.....	D −.123	−.110	.165	.089	D .135	.362
Degree of crinkly	D .068	.....	.232	.....	−.290	.....	.445	.....	.502	.....	−.368	.....	.....	.....	D −.166	.....	.275	.....	−.234	.....
Degree of lobing	−.039	.....	.249	.....	−.454	.....	.534	.....	.674	.....	−.430	.....	.....	.....	D −.103	.....	.010	.....	−.269	.....
Degree of color	−.123	.....	.036	.....	−.394	.....	.512	.....	.586	.....	−.419	.....	.....	.....	D −.144	.....	.196	.....	−.155	.....
Alicole index	D −.008	.084	−.080	.....	.093	.288	−.352	−.217	−.231	−.198	.013	.278	.....	.....	−.033	−.032	−.252	−.032	.047	.281
Type of plant	−.331	.....	.404	.....	−.883	.....	.619	.....	.928	.....	−.899	.....	.224	.....	D −.284	.....	−.082	.....	−.497	.....

* Coefficients preceded by the letter "D" are those in which characters derived from different parents tend to remain associated. F_2 coefficients in excess of 0.150 are greater than three times their error. F_1 coefficients in excess of 0.257 are greater than three times their error.

TABLE II.—*Coefficients of correlation among the characters of the plants of the first and second generations of the hybrid between crinkly maize and Florida teosinte*—Continued

Character.	Length ear stalk, best infl.		Length ♀ portion, best infl.		Branches on best infl.		Rows terminal spike, best infl.		Position of best spike.		Length of best spike.		Rows of alicoles on best spike.		Double ♀ alicoles on best spike.		Single ♀ alicoles on best spike.	
	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1
Height	.365	.503	−.014	−.318	.248	.352	D .050	.408	D −.075	.349	.344	−.435	D .057	−.032	D .037	−.251	.169	−.014
Height of tallest sucker	.409	.355	−.139	−.208	.272	.185	D .109	.237	D −.186	.247	D .207	−.348	D .056	−.162	−.123	−.063	.114	−.127
Total sucker height	.660	.330	−.330	−.231	.367	.089	D .045	.182	D −.106	.233	D −.180	−.165	D .000	.179	−.261	−.233	.476	.071
Number of suckers	.374	−.084	−.241	−.045	.159	−.070	−.010	−.145	D −.046	.084	−.253	−.089	−.000	.022	−.229	−.010	.123	−.010
Leaves above	−.026	.063	.310	−.004	D .041	−.089	D .222	.071	D .030	−.077	.306	.017	.220	−.045	.169	.089	D .044	−.010
Total number of leaves	D −.000	.544	−.064	.233	.092	.351	−.081	.173	D −.218	.193	.093	−.247	−.085	−.084	−.191	−.198	.033	−.014
Length of branching space	.275	.110	D .122	−.045	.291	.171	.127	.134	D .017	−.077	.224	−.017	D .238	.063	D .067	−.077	.206	−.045
Length of central spike	.162	.320	.166	.089	D .000	.230	.216	−.100	D .066	.100	.244	−.145	.169	.032	.039	−.105	D .243	.071
Length of longest tassel branch	.313	.247	−.024	−.303	.173	.237	.000	−.077	.098	.077	.207	.158	.026	−.134	−.091	.095	.183	−.006
Length of glume	.126	.266	D .048	−.045	.055	.145	D .151	.028	.049	−.027	.061	−.155	−.028	.084	−.082	−.063	.091	.123
Number of tassel branches	.227	−.165	−.096	.185	.418	−.025	D .090	−.063	D −.141	.020	.157	.084	D .089	−.071	−.020	.045	.069	.142
Rows in central spike	−.069	.....	.115	.....	D .076	.....	.214	.....	−.050	.....	.035	.....	.277	.....	.032	.....	.131	.....
Length of leaf	.285	.313	−.066	.142	.269	.255	.000	.105	D −.066	.203	.180	−.055	−.040	.110	−.165	−.272	.098	.300
Width of leaf	−.120	−.230	.118	−.145	−.026	−.198	.240	.152	−.125	.032	.262	−.055	.137	.110	.269	.190	D .033	−.237
Width index	−.250	−.338	.102	−.170	−.183	−.290	.166	.055	−.054	−.138	.079	−.007	.121	.142	.287	.292	−.049	−.340
Length of sheath	.246	−.008	−.022	.055	.205	.232	D .020	−.114	D −.028	.321	D .161	−.030	D .063	.119	−.208	−.224	.178	.272
Position of longest leaf	D −.022	.089	−.069	−.008	.128	.134	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
Leaves above best inflorescence	D .174	.063	.092	−.095	D .082	−.017	D −.056	.247	D .017	.155	.173	.251	D −.046	−.142	.014	.045	−.075	.027
Leaves on best inflorescence	D .236	.084	.111	−.182	D .101	.045	.182	.152	D .063	.247	.129	.219	.197	.063	.177	.105	.....	.077
Length of best inflorescence	.961	.973	−.350	−.359	.492	.624	D .075	.077	.125	−.239	D .010	.285	−.048	.235	−.069	−.347	.020	.287
Length ear stalk, best inflorescence	.....	.....	−.465	−.326	.528	.560	D .017	.110	.080	−.171	−.112	.257	−.079	.119	−.165	−.281	.033	.212
Length ♀ portion, best inflorescence	−.465	−.326	.....	.....	−.510	−.348	.205	−.114	D .241	.100	.169	−.205	.301	−.027	.435	.219	D .099	−.055
Number branches on	.528	.560	−.510	−.348	.....	.....	−.100	.149	D −.115	−.239	−.045	.228	−.081	.315	−.149	−.438	D −.010	.350
Rows terminal spike, best inflorescence	D .017	.010	.205	−.114	−.100	.149	.....	.....	D −.014	.032	.207	−.134	.601	−.155	.355	.185	D .094	−.028
Position of best spike	.080	−.171	D .241	−.100	D −.115	−.239	−.014	.032	.....	.....	.074	−.207	D .032	−.205	D .215	−.032	D −.020	−.123
Length of best spike	−.112	.257	.169	−.205	−.045	.228	.207	−.134	D .074	−.207	.....	.....	.141	.017	.471	.077	D −.010	.324
Rows of alicoles on best spike	−.079	.119	.301	−.027	−.081	.315	.601	−.155	D .032	−.205	.141	.017	.....	.....	.242	−.504	.137	.586
Double ♀ alicoles on best spike	−.165	−.281	.435	.219	−.149	−.438	.355	.185	D .215	−.032	.471	.077	.242	−.504	.....	.....	−.512	−.726
Single ♀ alicoles on best spike	.033	.212	D .099	−.055	D −.010	.350	D .094	−.028	D −.020	−.123	−.010	.324	D .137	.586	−.512	−.726	.....	.....
Spikes in prophyllary	.339	.182	−.366	.247	.192	.251	D .133	−.055	D −.130	.055	D −.162	−.365	−.210	.123	−.267	−.152	D −.010	−.009
Days to pollen	.048	.182	−.232	−.168	.146	.323	−.456	.032	D −.081	.193	−.185	−.028	−.356	.032	−.494	−.307	.075	.259
Days to silk	.....	.....	.....	.....	.....	.....	−.415	.045	D −.047	.233	−.092	−.127	−.317	.084	−.419	−.394	.069	.224
Days pollen to silk	D .086	.375	.085	−.342	D .212	.485	.207	.045	D .111	.207	.315	−.226	.161	.045	.297	−.378	−.024	.077
Degree of crinkly	−.229	.....	.179	.....	−.156	.....	.301	.....	−.022	.....	.182	.....	.309	.....	.267	.....	D .114	.....
Degree of lobing	−.265	.....	.188	.....	−.145	.....	.088	.....	−.035	.....	.076	.....	.118	.....	.245	.....	−.042	.....
Degree of color	−.138	.....	.182	.....	−.170	.....	.224	.....	D .010	.....	.086	.....	.247	.....	.295	.....	−.014	.....
Alicole index	.075	.200	−.461	−.114	−.149	.442	−.070	−.228	D −.169	−.014	D −.169	.055	D .163	.650	−.704	−.915	.806	.862
Type of plant	−.247	.....	.214	.....	−.257	.....	.110	.....	D .097	.....	D −.099	.....	.131	.....	.442	.....	−.204	.....

Character.	Number of spikes in prophyllary.		Alicole index.		Days to pollen.		Days to silk.		Days pollen to silk.		Degree of crinkly.		Degree of lobing.		Degree of color.		Type of plant.	
	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2	F_1
Height	.280	.267	.755	.134	.155	.257	.200	.335	D .131	.327	—.177	.....	—.256	.....	—.249	.....	—.628	.....
Height of tallest sucker	.318	.279	.460	—.071	.149	.300	.174	.369	D .065	.330	—.061	.....	—.239	.....	—.140	.....	—.458	.....
Total sucker height	.380	.193	.572	.127	.067	.145	.032	.176	—.115	.158	—.150	.....	—.204	.....	—.073	.....	—.444	.....
Number of suckers	.259	.055	.519	—.006	D —.083	—.292	D —.128	—.329	—.125	—.257	—.143	.....	—.235	.....	D .014	.....	—.334	.....
Leaves above	—.116	.100	—.066	—.045	—.206	.138	—.176	.032	.124	—.142	D —.027	.....	D —.042	.....	D —.061	.....	D —.181	.....
Total number of leaves	.048	.458	.060	.045	.536	.573	.544	.607	—.046	.416	—.131	.....	—.086	.....	—.217	.....	—.445	.....
Length of branching space	.068	—.084	.229	.020	D —.052	.182	.043	.185	D .313	.114	—.078	.....	—.186	.....	—.137	.....	—.452	.....
Length of central spike	—.010	.305	D .134	.105	—.206	.420	—.160	.505	.172	.439	D —.131	.....	D —.157	.....	.000	.....	D —.316	.....
Length of longest tassel branch	.207	.123	.282	—.045	D —.000	.017	.066	.055	D .225	.095	—.267	.....	—.447	.....	—.238	.....	—.731	.....
Length of glume	.036	.142	.140	.077	D —.068	.063	D —.094	.105	D —.059	.131	—.184	.....	—.080	.....	—.044	.....	—.300	.....
Number of tassel branches	.037	—.084	D —.008	.084	.171	—.155	.....	.....	D .308	—.005	D .068	.....	—.039	.....	—.123	.....	—.331	.....
Rows in central spike	—.122	.....	—.080	.....	—.105	.....	.....	.....	.114	.....	.233	.....	.249	.....	.036	.....	.404	.....
Length of leaf	.177	.030	.093	.288	.302	.055	.....	.....	D .032	.138	—.290	.....	—.454	.....	—.394	.....	—.883	.....
Width of leaf	—.094	—.155	—.352	—.217	—.355	—.354	.....	.....	.151	—.226	—.445	.....	.534	.....	.512	.....	.619	.....
Width index	—.141	—.134	—.231	—.198	—.425	—.294	.....	.....	.095	—.243	.502	.....	.674	.....	.586	.....	.928	.....
Length of sheath	.075	.105	.013	.278	.207	.114	.....	.....	D .138	.182	—.368	.....	—.430	.....	—.419	.....	—.899	.....
Position of longest leaf	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.224	.....
Leaves above best inflorescence	—.028	.095	—.033	—.032	D .127	.217	.....	.....	D —.123	—.110	D —.166	.....	D —.103	.....	D —.144	.....	D —.284	.....
Leaves on best inflorescence	D .014	—.212	—.252	—.032	—.190	.123	.....	.....	.165	.089	.275	.....	.010	.....	.196	.....	—.082	.....
Length of best inflorescence	.324	.195	.047	.281	.014	.168	.....	.....	D .135	.362	—.234	.....	—.269	.....	—.155	.....	—.497	.....
Length ear stalk, best inflorescence	.339	.182	.075	.200	.048	.182	.....	.....	D .086	.375	—.229	.....	—.265	.....	—.138	.....	—.347	.....
Length ♀ portion, best inflorescence	—.366	.247	—.461	—.114	—.232	—.168	.....	.....	.085	—.342	.179	.....	.188	.....	.182	.....	.214	.....
Number branches on best inflorescence	.192	.251	.149	.442	.146	.323	.....	.....	D .212	.485	—.156	.....	—.145	.....	—.170	.....	—.257	.....
Rows terminal spike, best inflorescence	D .133	—.055	—.070	—.228	—.456	.032	—.415	.045	.207	.045	.301	.....	.088	.....	.224	.....	.110	.....
Position of best spike	D —.130	.055	D —.169	—.014	D —.081	.193	D —.047	.233	D .111	.207	—.022	.....	— 035	.....	D .010	.....	.097	.....
Length of best spike	D —.162	—.365	D —.169	.055	—.185	—.028	—.092	—.127	.315	—.226	.182	.....	.076	.....	.086	.....	D —.099	.....
Rows of alicoles on best spike	—.210	.123	D .163	.650	—.356	.032	—.317	.084	.161	.045	.309	.....	.118	.....	.247	.....	.131	.....
Double ♀ alicoles on best spike	—.267	—.152	—.764	—.915	—.494	—.307	—.419	—.394	.297	—.378	.267	.....	.245	.....	.295	.....	.442	.....
Single ♀ alicoles on best spike	D —.010	—.009	.806	.862	.075	.259	.069	.224	—.024	.077	D .114	.....	—.042	.....	—.014	.....	—.204	.....
Spikes in prophyllary	.....	.....	.360	.105	.136	.364	.095	.390	—.157	.276	—.107	.....	—.203	.....	—.183	.....	—.327	.....
Days to pollen	.136	.364	.031	.253	.....	.....	.948	.908	—.275	.400	—.317	.....	—.270	.....	—.460	.....	—.473	.....
Days to silk	.095	.390	D —.099	.344	.948	.908	.....	.....	D .032	.748	—.283	.....	—.272	.....	—.479	.....	—.495	.....
Days pollen to silk	—.157	.276	—.414	.290	—.275	.400	D .032	.748	.....	.....	.150	.....	.024	.....	.022	.....	D —.012	.....
Degree of crinkly	—.107	.....	—.115	.....	—.317	.....	—.283	.....	.150	.....	.....	.....	.348	.....	.480	.....	.722	.....
Degree of lobing	—.203	.....	—.169	.....	—.270	.....	—.272	.....	.024	.....	.348	.....	.....	.....	.495	.....	.872	.....
Degree of color	—.183	.....	—.004	.....	—.460	.....	—.479	.....	.022	.....	.480	.....	.495	.....	.....	.....	.756	.....
Alicole index	.360	.105	.....	.....	.031	.253	D —.099	.344	—.414	.290	—.115	.....	—.169	.....	—.004	.....	—.448	.....
Type of plant	—.327	.....	—.448	.....	—.473	.....	—.495	.....	D —.012	.....	.722	.....	.872	.....	.756	.....	.....	.....

Since the correlations are given for both the F_1 and the F_2 populations, it seems unnecessary to discuss them in detail. An examination of the coefficients in Table II will show that many of the characters of maize tend to remain associated in inheritance, and a comparison of the coefficients in this table with those given in Table X for the brachytic hybrid and with those given in Table III of the Tom Thumb hybrid show also that the associated complex of characters is not the same for these three hybrids. Thus, it is apparent that the combination of the large number of suckers of teosinte with the multiple-rowed condition of the pistillate inflorescence of maize can be obtained more readily in the hybrid with crinkly ($r = -0.000$) than in that with brachytic, ($r = -0.202$), though this condition could not have been anticipated from the characteristics of the maize parents. From the practical standpoint of establishing combinations of the desirable characters of both species, this difference in the degree of relationship among the various characters in the several hybrids is encouraging in that it affords a basis for predicting that even where pronounced correlations are encountered between characters which it is desirable to separate, further hybrids with other varieties of maize probably will reveal weaker associations between these characters. In addition to the many instances of coherence, a study of Table II will show many inconsistencies between the F_1 and the F_2, as well as several disherences which can not be explained satisfactorily in the light of our present knowledge. These must await further investigations for proper interpretation.

TABLE III.—*Coefficients of correlation between the characters commonly affected in the modification of normal maize plants to those of the crinkly type*[a]

	Height.	Central spike.	Branching space.	Number of branches.	Length of longest branch.	Length of blade.	Width of blade.	Width index.	Length of sheath.	Degree crinkly.[b]	Degree lobing.[b]	Degree color.[b]	Generation.
Central spike.....	0.335												F_2
	.119												F_1
Branching space..	.570	0.195											F_2
	.145	−.032											F_1
Number of branches.	.464	.126	0.542										F_2
	−.089	−.323	−.055										F_1
Length of longest branch.	.618	.622	.549	0.361									F_2
	.055	.063	.114	.247									F_1
Length of blade...	.694	.205	.480	.438	0.530								F_2
	.441	.134	.257	.073	−.105								F_1
Width of blade...	−.041	.014	−.040	D. 130	−.130	−0.251							F_2
	−.193	−.440	−.030	.245	.171	−.235							F_1
Width index.....	−.434	−.127	−.320	−.172	−.417	−.746	0.788						F_2
	−.327	−.378	−.149	.138	.171	−.691	.860						F_1
Length of sheath..	.508	.373	.391	.330	.531	.671	−.388	−0.646					F_2
	.228	.187	.171	.164	.179	.530	.342	−.542					F_1
Degree of crinkly [b]	−.177	−.131	−.078	D. 068	−.267	−.290	.445	.502	−0.368				F_2
Degree of lobing [b].	−.256	−.157	−.186	−.039	−.447	−.454	.534	.674	−.430	0.348			F_2
Degree of color [b].	−.249	.000	−.137	−.123	−.238	−.394	.512	.586	−.419	.480	0.495		F_2
Type of plant [b, c].	−.628	−.316	−.452	−.331	−.711	−.883	.619	.928	−.899	.722	.872	0.756	F_2

[a] The coefficients are shown for both F_1 and F_2. Negative coefficients (indicated by a minus sign) apply to those cases in which a high value for one character is correlated with a low value for the other. F_1 coefficients greater than 0.257 are in excess of three times the error. F_2 coefficients greater than .150 are significant. Coefficients indicated by D represent disherences.

[b] These characters are not found in the F_1.

[c] The coefficients with type of plant are calculated by the formula for biserial correlation. Biserial coefficients greater than 0.186 are in excess of three times the error.

CORRELATIONS BETWEEN CRINKLY CHARACTERS

The characters which are involved primarily in the modification of normal plants to those of the crinkly type have been assembled in Table

III. In attempting to determine to what extent the crinkly complex of characters tends to remain in combination it is desirable to eliminate as far as possible the correlations expected on physiological grounds. Thus there are logical and experimental reasons for expecting physiological correlations of height with the five following characters given in Table III: Central spike, branching space, number of branches, length of longest branch, and length of blade. The nature of the crinkly teosinte cross is such as also to provide genetic causes of correlations of height with these characters, but with width of leaf genetic factors presumably operate in one direction while physiological factors operate in the other.

Thus, the crinkly variation has short stalks and wide leaves as compared with teosinte, and if there is a genetic correlation between these characters a negative correlation between height and width of leaves would be expected in the F_2. Further, since physiological factors normally tend to produce a positive correlation between height and width of leaves, the net effect of genetic and physiological factors operating in opposite directions would be to reduce the correlation essentially to zero. This is the observed result, though the coefficient is negative ($r = -0.041$), indicating possibly that the genetic factors were somewhat more effective than the physiological factors in bringing about the observed relationship.

When the correlation between these two characters of the F_1 plants is examined it also is found to be negative. While the correlation is not significant, its departure from the 0.2 or 0.3 usually obtained with these characters and the fact that the correlation with leaf index also is negative seem to require some explanation. It can be assumed that some peculiar environmental condition caused an increase in height and an actual and relative decrease in width of leaf such as obtain under extreme conditions where the plants become spindling; but such an hypothesis can not be accepted with favor when the exceptionally sturdy nature of the plants is taken into account.

The alternative is to attribute the results to genetic causes. Thus, if either the crinkly or the teosinte parent were heterozygous for a dominant factor which controlled a character complex of height, length, and width of blade, and the corollary height factors, length of central spike and branching space, then the F_1 in effect would be a back cross of this nature and the observed F_1 correlations would be obtained. While such a condition is not beyond the realm of possibility, it certainly seems singular that the complex of characters involved is so essentially that by which the recessive variation crinkly differs from the normal form.

It may be less unreasonable to assume that in hybrids such as this, where a general blending of the characters takes place, occasionally in certain plants one parental type or the other becomes partially dominant. There then would be F_1 individuals in which all the maize characters would be raised somewhat above the mean, and others in which they would be below the mean. Such behavior would result in a population consisting largely of plants intermediate between the parents, but with the tails of the distribution made up of the parental character combinations, being those cases where the threshold of dominance had been crossed. The second generation of these several F_1 plants need not necessarily behave very differently, and the F_1 correlations would be provided for.

It is well known that the degree of dominance is extremely variable, but this variability formerly has been thought of in connection with individual characters. There is evidence from other sources that variations

in dominance are constitutional, affecting many or all of the characters. A striking instance is afforded by hybrids between maize and *Euchlaena perennis*. In these hybrids there is a much higher degree of dominance of all the teosinte characters than has been found in hybrids with *E. mexicana*.

Regarding the three characters graded for the degree of resemblance to the crinkly parent and their relations to the measured characters and to themselves, since in these cases there was no variation in the F_1 plants, all being normal, there can be no F_1 correlations.

Taking up the degree of crinkly which represents an attempt to measure the wrinkling of the leaf blade, this character is found in the F_2 to be significantly correlated with eight of the eleven characters and with the type of plant as arbitrarily classed. These correlations, some of them large, are all in the direction of coherences.

The degree of lobing which evaluates the amount of lobing at the base of the leaf is found to be associated with ten other characters and with the type of plant, while the degree of color is correlated with eight characters and with plant type.

Although only a few of these correlations are large, they indicate that the crinkly complex of characters forms a correlated group suggesting loose linkage.

Since the plants were classed into crinkly and noncrinkly from their general appearance, it becomes of interest to discover to what extent the three characters, leaf lobing, crinkling, and color, determined the class in which the plants were placed. From an examination of Table III it is found that the degree of lobing, the least conspicuous of the three characters, has the closest correlation with the type of plant, but that this correlation is not as close as that of width index with type of plant, this index being a measured character. It would appear, therefore, that the relative width of the leaves was an important factor in the classification of the plants.

Since general characteristics were considered in classifying the plants into two groups, it may be urged with reason that it was a combination of the degree of crinkly, lobing and color that influenced judgment in classifying the plants. To test this, the grades of the three characters were combined in several ways and the correlations of these various combinations with plant class calculated. The coefficients are given with the frequency polygons in figures 40 to 43. It is found that the combination of degree of crinkly with degree of lobing is very closely correlated with plant class, the coefficient being $r=0.99 \pm 0.03$, the highest obtained with type of plant. While it is apparent that any plant having a high degree of crinkly and lobing would almost certainly be classed as crinkly, it is clear also that these two characters are not closely correlated; $r=0.348$. The regressions are 0.181 ± 0.029 and 0.669 ± 0.109 grades. Thus, for each change of one degree in the amount of crinkly there is a change of 0.18 degree in the amount of lobing, while for each change of degree of lobing there is a corresponding change of 0.67 degree in the amount of crinkly.

CORRELATION OF THE CRINKLY VARIATION WITH CHARACTERS OF MAIZE

Since all of the characters which are thought to be involved in the crinkly variations show significant correlations with type of plant, it seems reasonable to consider this arbitrary grouping as representing a definite segregation. The very high degree of correlation with leaf

index, however, is a cause for some misgiving, since it indicates a tendency on the part of the observer to class short, wide-leafed plants as crinkly. With this reservation in mind, the biserial correlations of the various characters with plant type may be examined. Arranging the characters in the order of their degree of correlation with type of plant, the ranking shown in Table IV is obtained.

TABLE IV.—*Biserial correlations of crinkly type of plant with the characters named*[a]

Rank.	Character.	Correlation.
1	Width index	0.928
2	Length of sheath	−.899
3	Length of leaf	−.883
4	Degree of lobing	.872
5	Degree of color	.756
6	Degree of crinkly	.722
7	Length of longest tassel branch	−.711
8	Height	−.628
9	Width of leaf	.619
10	Length of best inflorescence	−.497
11	Days to silk	−.495
12	Days to pollen	−.473
13	Height of tallest sucker	−.458
14	Length of branching space	−.452
15	Alicole index	−.448
16	Total number of leaves	−.445
17	Total sucker height	−.444
18	Number double ♀ alicoles	.442
19	Tassel branch index	.426
20	Rows in the central spike	.404
21	Number of suckers	−.334
22	Number of tassel branches	−.331
23	Number of spikes in prophyllary	−.327
24	Length of central spike	−.316
25	Length of glume	−.300
26	Leaves above best inflorescence	−.284
27	Number of branches on best inflorescence	−.257
28	Length of ear stalk of best inflorescence	−.247
29	Position of longest leaf	.224
30	Length ♀ portion of best inflorescence	.214
31	Number single ♀ alicoles	−.204
32	Leaves above uppermost branch	−.181
33	Number rows of alicoles on best spike	.131
34	Rows in terminal spike of best inflorescence	.110
35	Length of best spike	−.099
36	Position of best spike	.097
37	Leaves on best inflorescence	−.082
38	Central spike index	−.017
39	Days pollen to silk	.012

[a] Coefficients above .186 are in excess of three times the error. Correlations 26, 32, 35, 36, and 39 are disherences.

The last 8 coefficients in this table may be disregarded, since they are less than three times their error. Of the others, 16 are characters which enter either directly or clearly indirectly into the classification of type of plant. Thus, height of plant doubtless was a factor which influenced classification, and for this reason such characters as total sucker height and number of suckers (both of which are correlated with height and in a sense simply are other measures of height) also are expected to be correlated with plant type. Eliminating such relationships as these, there are left 16 coefficients greater than three times their errors. A further reduction is possible with these 16, owing to the fact that in some instances

there are two or more measures of the same character. For instance, days to pollen and days to silk both obviously measure the same thing—season, while alicole index, number of double female alicoles and number of single female alicoles form another intercorrelated group, measuring essentially the same thing. With all such cases considered and reduced to a single coefficient, there remain 13 characters which are correlated directly with type of plant. These are given in italics in the last column of Table IV.

Of these 13 characters 12 are coherences showing a tendency for maize characters to be associated with the crinkly type of plant, while one is a disherence. This disherence is with leaves above the best inflorescence. Thus the crinkly plants have fewer nodes above the best lateral inflorescence than do the noncrinklies; a condition the reverse of that of the parental combination. In view of this fact it may be well to examine all the correlations with the character "leaves above the best inflorescence" shown in Table II.

In the second generation there are 36 possibilities for correlations with the character "leaves above best inflorescence," and 26 of these indicate disherences. Of the 36 coefficients, 17 are in excess of three times the error, but when the F_1 correlations are considered and the physiological correlations eliminated, these 17 are reduced to 12. Of the 12 correlations the one dealing with leaves above the upper branch may be eliminated on morphological grounds, leaving 11, of which 10 are disherences. These disherent correlations are concerned with the following characters:

1. Height.
2. Rows in central spike.
3. Length of leaf.
4. Width of leaf.
5. Width index.
6. Position of longest leaf.
7. Leaves on best inflorescence.
8. Rows in terminal spike of best inflorescence.
9. Degree of crinkly.
10. Type of plant.

It may be of some significance that, of these 10, 6 are characters involved in the crinkly variation. It will be recalled that there is a tendency among crinkly plants to develop ears at the base of the tassel or in the axil of the upper leaf, and it seems not improbable that this tendency is manifested in the present hybrid. If this be true, it follows that the coefficients observed are coherences rather than disherences, since the character of few leaves above the upper branch becomes another measure of the crinkly variation. In the cross between Tom Thumb maize and Florida teosinte there were no significant disherences with the number of nodes above the uppermost inflorescence; a fact indicating that this character was associated with other characteristics of maize.

It may be concluded that "few leaves above the best inflorescence" in this case is a characteristic of the crinkly variation; it follows that all eight of the characters of maize not directly involved in the classification of the plants are correlated with the crinkly type.

It may be urged that while a character such as total leaves would not influence directly the classification of plants into two types, it might become correlated with type simply as a secondary relationship through its association with height. If this were true, the partial correlation of type with total leaves for constant height should be zero, when it actually is $r = -0.433 \pm 0.059$.

It seems clear that such characters as season, total leaves and the several measures of the inflorescences all are correlated with the variation known as crinkly, though none are characters by which the crinkly type is differentiated from the normal, and their correlation with type is not due to their association with some one crinkly characteristic.

Since the amount of leaf lobing was closely correlated with the crinkly type, and, furthermore, since this character would be expected to have little weight in the classification of plants, it may be well to examine the correlations of this character with all others. These correlations are given in Table V. With this character the usual correlation formula can be applied with but two exceptions—type of plant and alicole index. As in Table IV, the characters are arranged in the order of their degree of relationship with the lobing of the leaves. Thirteen of the 36 coefficients are less than three times their errors; of these, seven were significantly correlated with plant type, but not one of the seven is significantly correlated with the degree of leaf lobing.[6]

TABLE V.—*Product moment correlations of the degree of lobing with the characters named*[a]

Rank.	Character.	Correlation.
1	Type of plant	[b] 0.872
2	Leaf index	.674
3	Width of leaf	.534
4	Degree of color	.495
5	Length of leaf	−.454
6	Length of longest tassel branch	−.447
7	Length of sheath	−.430
8	Degree of crinkly	.348
9	Days to silk	−.272
10	Days to pollen	−.270
11	Length of best inflorescence	−.269
12	Length of ear stalk of best inflorescence	−.265
13	Height	−.256
14	Rows in the central spike	.249
15	Number double ♀ alicoles	.245
16	Height of tallest sucker	−.239
17	Number of suckers	−.235
18	Total sucker height	−.204
19	Number of spikes in prophyllary	−.203
20	Length ♀ portion of best inflorescence	.188
21	Length of branching space	−.186
22	Alicole index	[b] −.169
23	Length of central spike	−.157
24	Number of branches on best inflorescence	−.145
25	Number of rows alicoles on best spike	.118
26	Leaves above best inflorescence	−.103
27	Rows in terminal spike of best inflorescence	.088
28	Total number of leaves	−.086
29	Length of glume	−.080
30	Length of best spike	.076
31	Number of single ♀ alicoles	−.042
32	Leaves above	−.042
33	Number of tassel branches	−.039
34	Position of best spike	−.035
35	Days pollen to silk	.024
36	Leaves on best inflorescence	.010

[a] Coefficients in excess of 0.150 are greater than three times the error. [b] Biserial correlations.

[6] There were eight coefficients with type of plant which were less than three times their error, but one of these, that with central spike index, does not appear in the correlation with the degree of lobing. It was omitted from all product moment correlations to facilitate the calculations by means of punched cards. The available cards were too short to accommodate all the characters.

The correlation between the rank of the characters in regard to correlation with type of plant and their rank in regard to correlation with degree of lobing is 0.21 ± 0.11, which is not a very close agreement. Not only are the characters not correlated with the degree of lobing in the same order as with type of plant, but the degree of relationship also is much weaker with lobing than with plant type. In general, however, characters of maize not involved in the crinkly variation are found correlated with the crinkly character lobing, clearly indicating genetic linkage of these numerous maize factors with the gene for crinkly.

RAMOSE × TEOSINTE

Ramose is a variation in which the simple pistillate inflorescence of maize has been replaced by a compound structure somewhat resembling the tassel. Practically all the seed is borne on branches, the central axis bearing seeds only at the apex. In addition to the branched condition of the ear, the number of branches on the staminate inflorescence has been increased at the expense of the central spike, the latter being reduced greatly in length. The branches of the tassel decrease regularly in length from the base to the tip, and there is little differentiation between branches and paired spikelets. This gradual decrease in the length of the branches gives the tassel a characteristic conical appearance easily distinguishable from the normal form.

The ramose variation, first described by Gernert, was found in a field of the Leaming variety (*9*), and has since been found in a strain of sweet corn grown by J. M. Mack of Fallbrook, Calif., (*12*). In crosses with normal maize this character behaves as a simple Mendelian recessive, and reappears essentially unaltered in the second generation. In the first hybrids studied the branched condition of the ear and tassel behaved as a single character, but in the strain of sweet corn grown by Mr. Mack plants were found having typical ramose tassels with normal unbranched ears, showing that the apparently single character was capable of subdivision or that separate modifying factors existed for each inflorescence.

The ramose ear and relatively unspecialized tassel, as compared with the normal maize inflorescences, represent a reversion to a primitive type in this one character, and its combination with the nearest wild relative of maize might be expected to shed additional light on the origin of the present single-spiked pistillate inflorescence of maize.

The hybrid with teosinte was made using ramose maize as the female parent. A few F_1 plants were raised in the greenhouse at Chula Vista, Calif., and the second generation to be discussed is the progeny of one of these plants. The remainder of the F_1 seed was planted in the field with the F_2, and resulted in 44 plants, all normal with respect to the form of inflorescence, which was similar to that of other F_1 maize-teosinte hybrids.

One hundred and nineteen F_2 plants were grown, of which 29 were classed as ramose, the percentage being 24.4 ± 2.7. One of these plants is shown in Plate 6, A, and the pistillate inflorescences are shown in Plate 7. The classification was made before the pistillate inflorescences were harvested, and therefore was based entirely on the characteristics of the tassel. In these hybrid plants almost every lateral branch terminates in a staminate panicle, and the ramose nature of the tassel is in evidence over the entire plant. The fact that these inflorescences are

developing over a relatively long period of time obviates some of the difficulties in classification arising from the effect on branching of fluctuating environmental factors.

CHARACTERS MEASURED

Several characters which were measured in the crinkly-teosinte hybrid were disregarded in the ramose hybrid, since the two parents were not strikingly different with respect to them, and several new characters which serve to differentiate the parents were added. The added characters are: (*a*) Length of upper branch of tassel; (*b*) best spike, double male; (*c*) best spike, mixed male and female; and (*d*) number of branches on the best spike.

LENGTH OF UPPER BRANCH OF TASSEL.—In ramose, the upper branch of the tassel often is but a centimeter or two long while in teosinte it usually exceeds 10 centimeters in length.

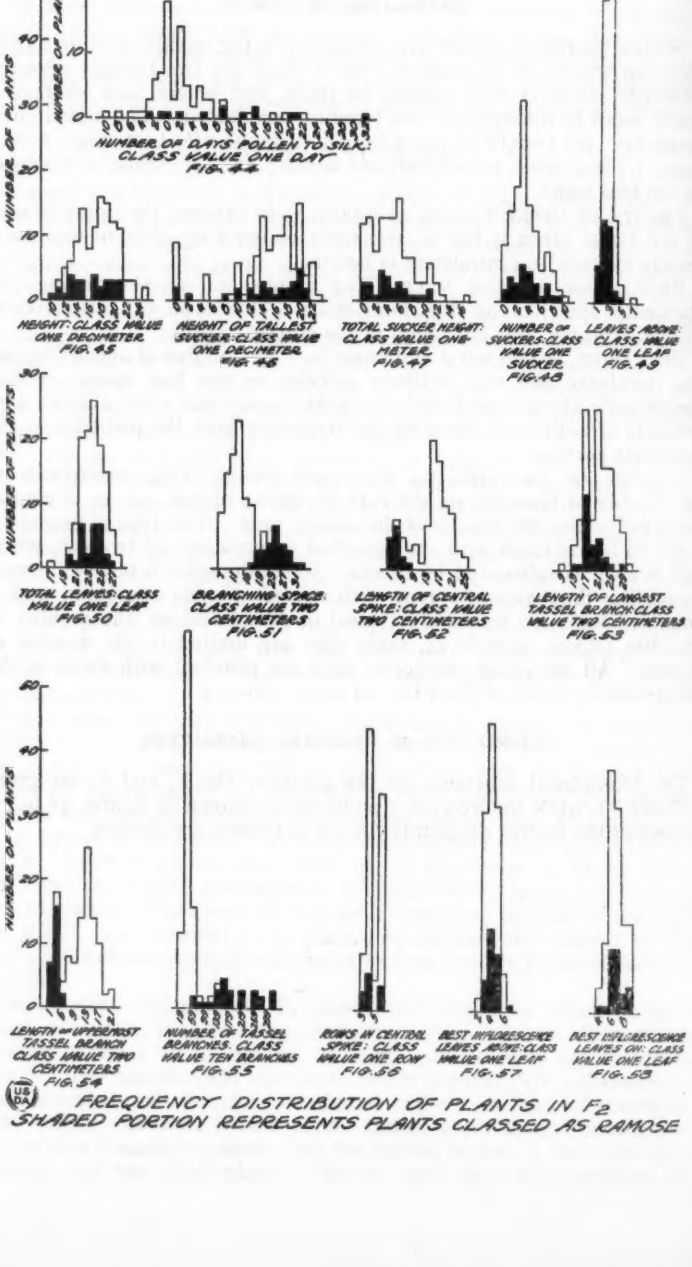
BEST SPIKE, DOUBLE MALE.—The number of alicoles having two staminate spikelets on the best spike. This type of inflorescence, though expected, was not found in the crinkly hybrid.

BEST SPIKE, MIXED MALE AND FEMALE.—The number of alicoles having one staminate and one pistillate spikelet on the best spike. Where double male alicoles are found, the spike usually has a few alicoles with spikelets of both sexes marking the transition from the pistillate to the staminate portion.

NUMBER OF BRANCHES ON THE BEST SPIKE.—This corresponds to the number of branches on the ears of ramose plants, and is, of course, found only when the plant is of the ramose type. This type of branching is not to be confused with the branched inflorescence of teosinte, where each branch is subtended by bracts. When the spike is but two-rowed, resembling the teosinte parent with respect to this character, and is combined with the branching typical of ramose maize, the number of branches seldom exceeds 14, since they are limited to the number of alicoles. All the other characters used are identical with those of the crinkly-teosinte hybrid described on pages 540–543.

INHERITANCE OF MEASURED CHARACTERS

The biometrical constants for the plants of the F_1 and F_2 are given in Table VI, while the frequency polygons are shown in figures 44 to 75. In each of the figures the plants classed as ramose are shaded.


NUMBER OF PLANTS
NUMBER OF DAYS POLLEN TO SILK: CLASS VALUE ONE DAY FIG. 44
HEIGHT: CLASS VALUE ONE DECIMETER. FIG. 45
HEIGHT OF TALLEST SUCKER: CLASS VALUE ONE DECIMETER. FIG. 46
TOTAL SUCKER HEIGHT: CLASS VALUE ONE METER. FIG. 47
NUMBER OF SUCKERS: CLASS VALUE ONE SUCKER. FIG. 48
LEAVES ABOVE: CLASS VALUE ONE LEAF FIG. 49
TOTAL LEAVES: CLASS VALUE ONE LEAF FIG. 50
BRANCHING SPACE: CLASS VALUE TWO CENTIMETERS FIG. 51
LENGTH OF CENTRAL SPIKE: CLASS VALUE TWO CENTIMETERS FIG. 52
LENGTH OF LONGEST TASSEL BRANCH: CLASS VALUE TWO CENTIMETERS FIG. 53
LENGTH OF UPPERMOST TASSEL BRANCH CLASS VALUE TWO CENTIMETERS FIG. 54
NUMBER OF TASSEL BRANCHES. CLASS VALUE TEN BRANCHES FIG. 55
ROWS IN CENTRAL SPIKE: CLASS VALUE ONE ROW FIG. 56
BEST INFLORESCENCE LEAVES ABOVE: CLASS VALUE ONE LEAF FIG. 57
BEST INFLORESCENCE LEAVES ON: CLASS VALUE ONE LEAF FIG. 58

FREQUENCY DISTRIBUTION OF PLANTS IN F_2
SHADED PORTION REPRESENTS PLANTS CLASSED AS RAMOSE

FIGURES 44 TO 58

FIG. 44.—Number of days pollen to silk; frequency distribution of plants in F_2. Class value, one day. Shaded portion represents plants classed as ramose.

FIG. 45.—Height; frequency distribution of plants in F_2. Class value, 1 decimeter. Shaded portion represents plants classed as ramose.

FIG. 46.—Height of tallest sucker; frequency distribution of plants in F_2. Class value, 1 decimeter. Shaded portion represents plants classed as ramose.

FIG. 47.—Total sucker height; frequency distribution of plants in F_2. Class value, 1 meter. Shaded portion represents plants classed as ramose.

FIG. 48.—Number of suckers; frequency distribution of plants in F_2. Class value, one sucker. Shaded portion represents plants classed as ramose.

FIG. 49.—Leaves above; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as ramose.

FIG. 50.—Total leaves; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as ramose.

FIG. 51.—Branching space; frequency distribution of plants in F_2. Class value, 2 cm. Shaded portion represents plants classed as ramose.

FIG. 52.—Length of central spike; frequency distribution of plants in F_2. Class value, 2 cm. Shaded portion represents plants classed as ramose.

FIG. 53.—Length of longest tassel branch; frequency distribution of plants in F_2. Class value, 2 cm. Shaded portion represents plants classed as ramose.

FIG. 54.—Length of uppermost tassel branch; frequency distribution of plants in F_2. Class value, 2 cm. Shaded portion represents plants classed as ramose.

FIG. 55.—Number of tassel branches; frequency distribution of plants in F_2. Class value, 10 branches. Shaded portion represents plants classed as ramose.

FIG. 56.—Rows in central spike; frequency distribution of plants in F_2. Class value, one row. Shaded portion represents plants classed as ramose.

FIG. 57.—Leaves above best inflorescence frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as ramose.

FIG. 58.—Leaves on best inflorescence frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as ramose.

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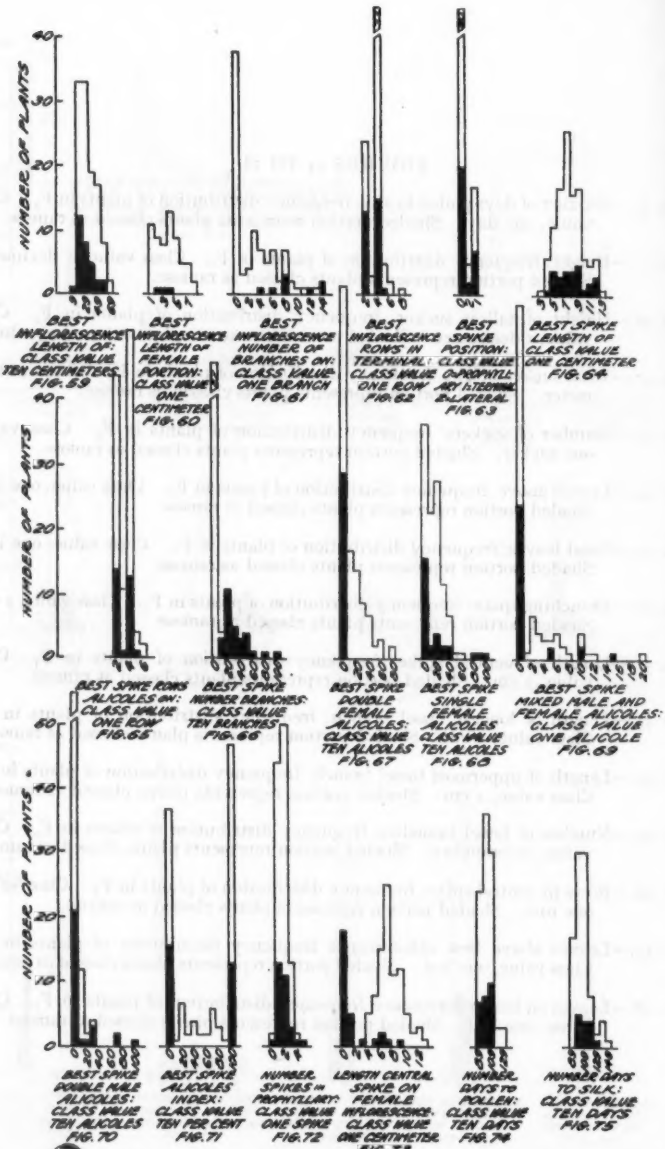

NUMBER OF PLANTS
0
10
20
30
40
BEST INFLORESCENCE LENGTH OF: CLASS VALUE TEN CENTIMETERS FIG. 59
BEST INFLORESCENCE LENGTH OF FEMALE PORTION: CLASS VALUE ONE CENTIMETER FIG. 60
BEST INFLORESCENCE NUMBER OF BRANCHES ON: CLASS VALUE ONE BRANCH FIG. 61
BEST INFLORESCENCE ROWS IN TERMINAL: CLASS VALUE ONE ROW FIG. 62
BEST SPIKE POSITION: CLASS VALUE O-PROPHYLLARY I-TERMINAL 2-LATERAL FIG. 63
BEST SPIKE LENGTH OF CLASS VALUE ONE CENTIMETER FIG. 64
BEST SPIKE ROWS ALICOLES ON: CLASS VALUE ONE ROW FIG. 65
BEST SPIKE NUMBER BRANCHES: CLASS VALUE TEN BRANCHES FIG. 66
BEST SPIKE DOUBLE FEMALE ALICOLES: CLASS VALUE TEN ALICOLES FIG. 67
BEST SPIKE SINGLE FEMALE ALICOLES CLASS VALUE TEN ALICOLES FIG. 68
BEST SPIKE MIXED MALE AND FEMALE ALICOLES: CLASS VALUE ONE ALICOLE FIG. 69
BEST SPIKE DOUBLE MALE ALICOLES: CLASS VALUE TEN ALICOLES FIG. 70
BEST SPIKE ALICOLES INDEX: CLASS VALUE TEN PER CENT FIG. 71
NUMBER SPIKES IN PROPHYLLARY: CLASS VALUE ONE SPIKE FIG. 72
LENGTH CENTRAL SPIKE ON FEMALE INFLORESCENCE: CLASS VALUE ONE CENTIMETER FIG. 73
NUMBER DAYS TO POLLEN: CLASS VALUE TEN DAYS FIG. 74
NUMBER DAYS TO SILK: CLASS VALUE TEN DAYS FIG. 75

FREQUENCY DISTRIBUTION OF PLANTS IN F_2
SHADED PORTION REPRESENTS PLANTS CLASSED AS RAMOSE

FIGURES 59 TO 75

FIG. 59.—Length of best inflorescence; frequency distribution of plants in F_2. Class value, 10 cm. Shaded portion represents plants classed as ramose.

FIG. 60.—Length of female portion of best inflorescence; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as ramose.

FIG. 61.—Number of branches on best inflorescence; frequency distribution of plants in F_2. Class value, one branch. Shaded portion represents plants classed as ramose.

FIG. 62.—Rows in terminal spike of best inflorescence; frequency distribution of plants in F_2. Class value, one row. Shaded portion represents plants classed as ramose.

FIG. 63—Position of best spike; frequency distribution of plants in F_2. Class value, 0 for prophyllary, 1 for terminal, 2 for lateral. Shaded portion represents plants classed as ramose.

FIG. 64.—Length of best spike; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as ramose.

FIG. 65.—Rows of alicoles on best spike; frequency distribution of plants in F_2. Class value, one row. Shaded portion represents plants classed as ramose.

FIG. 66.—Number of branches on best spike; frequency distribution of plants in F_2. Class value, 10 branches. Shaded portion represents plants classed as ramose.

FIG. 67.—Double female alicoles on best spike; frequency distribution of plants in F_2. Class value, 10 alicoles. Shaded portion represents plants classed as ramose.

FIG. 68.—Single female alicoles on best spike; frequency distribution of plants in F_2. Class value, 10 alicoles. Shaded portion represents plants classed as ramose.

FIG. 69.—Mixed male and female alicoles on best spike; frequency distribution of plants in F_2. Class value, one alicole. Shaded portion represents plants classed as ramose.

FIG. 70.—Double male alicoles on best spike; frequency distribution of plants in F_2. Class value, 10 alicoles. Shaded portion represents plants classed as ramose.

FIG. 71.—Best spike, alicole index; frequency distribution of plants in F_2. Class value, 10 per cent. Shaded portion represents plants classed as ramose.

FIG. 72.—Number of spikes in prophyllary; frequency distribution of plants in F_2. Class value, one spike. Shaded portion represents plants classed as ramose.

FIG. 73.—Length of central spike on female inflorescence; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as ramose.

FIG. 74.—Number of days to pollen; frequency distribution of plants in F_2. Class value, ten days. Shaded portion represents plants classed as ramose.

FIG. 75.—Number of days to silk; frequency distribution of plants in F_2. Class value, ten days. Shaded portion represents plants classed as ramose.

TABLE VI.—*Biometrical constants for the first and second generations of the ramose × teosinte hybrid*

Characters.	First generation.			Second generation.									Fig. number of frequency polygon.
				Entire population.			Ramose group.			Normal group.			Difference.	
	Mean.	σ	P. E.	Mean.	σ	P. E.	Mean.	σ	P. E.	Mean.	σ	P. E.		
Height	21.39	1.89	0.19	17.32	3.15	0.19	16.10	3.30	0.41	17.71	3.06	0.21	1.61± .46	45
Height of tallest sucker	19.50	3.58	.36	14.70	5.82	.36	14.62	5.91	.74	14.72	5.80	.41	.10± .85	46
Total sucker height	7.34	3.35	.34	4.83	3.48	.21	4.83	3.48	.44	4.83	3.48	.24	.00± .50	47
Number of suckers	4.66	2.03	.21	3.46	2.23	.14	3.69	2.34	.29	3.39	2.23	.16	−.30± .32	48
Leaves above	2.48	.53	.05	2.70	.91	.06	2.83	1.08	.14	2.66	.84	.06	−.17± .14	49
Total number of leaves	22.55	1.33	.14	23.76	1.75	.12	23.55	1.03	.13	23.83	1.94	.14	.48± .20	50
Length of branching space	16.45	2.45	.26	14.62	6.34	.40	24.15	3.99	.52	11.69	3.40	.24	−12.46± .57	51
Length of central spike	17.00	2.00	.22	13.26	6.38	.44	2.13	1.75	.31	15.37	4.48	.36	13.24± .48	52
Length of longest tassel branch	21.85	2.56	.28	20.47	4.24	.25	18.48	3.14	.41	21.08	4.36	.31	2.60± .52	53
Length of uppermost tassel branch	12.67	2.82	.30	9.81	5.38	.32	2.04	.96	.13	12.04	3.85	.27	10.0 ± .30	54
Number of tassel branches	37.88	6.26	.67	65.88	73.32	4.62	177.00	74.60	9.68	31.77	18.99	1.33	−145.23±9.68	55
Rows in central spike	4.00	.00	.00	4.60	1.24	.07	3.80	1.84	.32	4.75	1.04	.08	.95± .33	56
Leaves above best inflorescence	4.27	.71	.72	4.10	.95	.06	4.25	.87	.11	4.06	.94	.07	−.19± .14	57
Leaves on best inflorescence	6.02	.77	.80	6.73	1.29	.08	6.86	1.20	.15	6.69	1.28	.09	−.17± .17	58
Length of best inflorescence	35.90	11.68	1.22	28.44	12.97	.82	23.86	11.16	1.40	30.02	13.29	.92	6.16±1.68	59
Length of ♀ portion of best inflorescence	1.71	1.68	.18	2.06	2.37	.15	.31	.95	.12	2.67	2.41	.17	2.36± .20	60
Number branches on best inflorescence	4.10	1.81	.19	12.40	23.19	1.48	40.17	31.90	4.00	2.70	3.19	.22	−37.47±4.00	61
Rows in terminal spike of best inflorescence	4.00	.00	.00	3.66	1.01	.06	3.14	1.04	.13	3.84	.95	.07	.70± .14	62
Length of best spike	7.71	.86	.09	7.56	2.12	.14	7.83	.89	.11	7.47	1.99	.14	−.36± .17	64
Rows of alicoles on best spike	2.48	.72	.58	3.19	1.05	.07	3.03	1.04	.13	3.24	1.07	.07	.21± .14	65
Double ♀ alicoles on best spike	7.45	5.02	.53	10.52	16.55	1.06	.00	.00	.00	14.19	17.84	1.25	14.19±1.25	67
Single ♀ alicoles on best spike	12.83	7.56	.79	13.72	17.67	1.13	16.48	27.42	3.44	12.76	12.46	.87	−3.72±3.54	68
Alicole index, best spike	61.33	25.86	2.69	52.12	44.34	2.82	44.38	49.25	6.18	54.83	42.16	2.95	10.45±6.84	71
Double ♂ alicoles on best spike	.26	.73	.08	4.05	14.10	.90	12.10	25.25	3.17	1.24	3.93	.28	−10.86±3.14	70
Mixed ♀ ♂ alicoles on best spike	3.64	3.16	.33	1.77	3.57	.23	1.55	3.74	.47	1.84	3.51	.25	.29± .53	69
Number of spikes in prophyllary	2.48	.65	.07	1.75	.82	.05	1.66	.84	.11	1.78	.81	.06	.12± .14	72
Days to pollen	84.45	3.19	.32	96.92	10.80	.73	96.52	7.88	1.06	97.05	11.65	.93	−.53±1.41	74

Mixed ♀ alicoles on best spike	3.64	3.16	.33	1.77	3.57	.23	1.55	3.74	.47	1.84	3.51	.25	.29± .53	69
Number of spikes in prophyllary	2.48	.65	.07	1.75	.82	.05	1.66	.84	.11	1.78	.81	.06	.12± .14	72
Days to pollen	84.45	3.10	.32	96.92	10.80	.73	96.52	7.88	1.06	97.05	11.65	.93	.53±1.41	74
Days to silk	85.57	3.63	.38	100.48	13.21	.70	105.43	10.19	1.84	99.59	13.50	1.08	−5.84±2.13	75
Days pollen to silk	1.14	1.56	.16	3.08	6.72	.48	10.86	9.44	1.70	1.59	4.78	.38	−9.27±1.74	44
Length of central spike on ♀ inflorescence				5.86	3.38	.22	1.41	2.51	.32	7.43	1.94	.14	6.02± .35	73
Position of best spike				.24	.52	.03	.38	.61	.08	.19	.47	.03	−.19± .10	63
Number of branches on best spike				7.65	16.87	1.08	29.52	21.42	2.69	.01	.01	.0007	−29.51±2.69	66

Height is not a feature of the ramose variation, as it is of crinkly, and no bimodality in the various measures of this character was to be expected. The figures will facilitate a comparison of the distributions of the plants, with respect to these characters in this hybrid, with the distributions of the crinkly and brachytic hybrid.

A comparison of the distribution of the first six characters in the crinkly (fig. 1 to 6) and ramose hybrids (fig. 45 to 50) shows a striking similarity, and emphasizes the failure of the semidwarf stature of crinkly to behave as a simple character.

As in the case of the hybrid with crinkly, many F_2 plants of the ramose hybrid were proterogynous, though the mean number of days from pollen to silk for the whole population and for each of the two groups comprising it was a positive value.

Bimodality is evident in the distributions for the several characters indicating the type of staminate inflorescence (fig. 51 to 55), and a very high correlation with the ramose type also is apparent. It must not be overlooked, however, that in each case there are intermediate plants.

The frequency distributions that measure the branching of the pistillate inflorescence (fig. 61 and 66) also are bimodal, as well as the alicole index (fig. 71), which in this hybrid presents the best evidence as yet obtained for the discontinuous inheritance of this character. The F_1 plants have a high percentage of single female alicoles, showing a partial dominance of this teosinte characteristic over the maize parent, and bimodality of the F_2 is therefore not unexpected. The majority of the plants would be expected to have a high percentage of single female alicoles, which proves to be the case; and in this respect the ramose hybrid resembles the crinkly hybrid and, like it, differs from the hybrid with Tom Thumb (*5*).

It will be observed (fig. 67) that none of the plants classed as ramose had double female alicoles. This condition may be related to the almost complete sterility of these plants, especially as they approach teosinte in the character of the number of rows of alicoles. Of the very few seeds borne by these ramose plants, all were on inflorescences that approximated maize in the number of rows of alicoles, and none was borne by the plants which resembled teosinte. Several plants with branched pistillate inflorescences were found that had but two rows of alicoles; but these plants were so completely sterile that there was no evidence of even the formation of spikelets; and the feathery branches, though not at all succulent, suggest the sterile "cauliflower" inflorescence of the pod-ramose hybrid (*3*). (See Pl. 7.) In none of these two-rowed inflorescences was there found more than one branch from an alicole, though these inflorescences sometimes were ramified further.

The almost complete sterility of the ramose segregates of the teosinte hybrid would account partially for the high percentage of plants with single female alicoles; and it is not without significance from the standpoint of the origin of the ear, suggesting as it does that teosinte is even further specialized with respect to branched inflorescences than is maize.

This sterility indicates that the change of normal maize to the ramose condition is not in the nature of a reversion to teosinte. While it is possible to obtain a complete series of fertile forms connecting the pistillate teosinte inflorescence with the inflorescence of maize, and a similar series connecting the normal maize inflorescence with that of the ramose type, it is not possible so to connect the ramose inflorescence with that

of teosinte. The rudiments of intermediate structures are found, but they remain abortive and sterile.

It is a moot question whether the simple pistillate inflorescence of maize represents the loss of a more specialized branched condition or has come about through a still further specialization of a branched inflorescence in which the branches have become united. The ramose variation is the principal evidence in support of the former view, and it is clear that the branched condition of ramose maize had nothing in common with the branched inflorescence of teosinte. The incompatibility of the ramose form of branched inflorescence in combination with the other characters of the pistillate spike of teosinte seems all the more remarkable in view of the general tendency toward branching manifested throughout the teosinte plant, and including both vegetative and floral organs.

Although it might have been expected that the ramose variation would be correlated with maize characters and that few nonramose inflorescences with many rows of alicoles would be obtained, the contrary proved to be the case. Thus, while the number of F_2 individuals grown from the ramose hybrid was less than that of any of the other hybrids, the parental types of inflorescences characterizing the normal forms of the parent species were recovered more nearly than in other hybrids. The best approximation to a normal unbranched ear was found in the F_2 of the ramose hybrid, and an inflorescence typical of Durango teosinte also was obtained ,though no spikes were found in either the crinkly or ramose hybrids having seeds shaped like those of Florida teosinte (*4*). (See Pl. 7, D.)

Not only were maizelike unbranched pistillate inflorescences obtained, but even in the relatively small group of ramose plants branched ears were found closely approximating the ramose ears of maize. In none of the cases of maizelike ears, however, were the inflorescences as large as the normal ears of the variety from which the ramose parent was obtained, the longest ear being less than 15 cm. in length.

The group of ramose pistillate inflorescences embraced no other ancestral characters. Thus, as in maize, when fertile pistillate spikelets were produced, these always had the hardened outer glumes and reduced bractlike inner glumes characteristic of the spikelets of a maize ear. There was a tendency for the inflorescences to be staminate, but this largely is a measure of sterility, which was so pronounced in the ramose plants. Among the ramose inflorescences that approached the two-rowed teosinte spike, the specialized rachis, characteristic of the pistillate inflorescence of teosinte, is entirely lacking, the inflorescence resembling completely a branch of the staminate panicle, with the distance between the articulations greater than is the case in normal pistillate inflorescences.

CORRELATION OF THE RAMOSE VARIATION WITH CHARACTERS THAT DISTINGUISH MAIZE FROM TEOSINTE

When the biserial correlations with type of plant are examined there are found to be only eight coefficients exceeding three times their error. These coefficients are given in Table VII. The biserial method could not be applied to the characters that measured the degree of ramoseness, since the distribution of plants with respect to these characters was bimodal. Of the eight coefficients, five at first sight appear to be disherences, while only three, days pollen to silk, height, and length of

best inflorescence are coherences. Of the five coefficients which would seem to be disherences three are capable of another interpretation, the correlations with length of pistillate portion of best inflorescence, number of double staminate alicoles on best spike, and number of rows in the terminal spike of the best inflorescence. The almost complete sterility of the ramose plants acts in such a manner as to reduce the length of the pistillate portion of the best inflorescence, causing a negative correlation of ramose type with this character. The positive correlation with the number of double male alicoles on best spike also is a disherence as viewed from the standpoint of normal maize, but, again, the sterility of the pistillate inflorescence seems the true explanation. The failure to develop pistillate flowers was manifested in many cases by the production of staminate spikelets, and in some cases entire inflorescences were staminate. Sterility also seems the best explanation of the negative correlation with the number of rows of alicoles on the ternimal spike of the best inflorescence.

TABLE VII.—*Biserial correlations of ramose type with the characters named* [a]

Character.	Correlation.
Days pollen to silk	0.76
Length ♀ portion of best inflorescence	−.60
Number of double ♂ alicoles on best spike	.46
Rows in the central spike	.42
Rows in terminal spike of best inflorescence	−.41
Length of longest tassel branch	−.36
Height	−.30
Length of best inflorescence	−.28
Days to silk	.24
Position of best spike	.22
Alicole index	−.14
Height of tallest sucker	−.13
Number of single ♀ alicoles on best spike	.13
Number rows of alicoles on best spike	.12
Leaves above best inflorescence	.12
Length of best spike	.10
Number of spikes in prophyllary	−.09
Total number of leaves	−.09
Number of suckers	.08
Leaves on best inflorescence	.08
Leaves above upper branch	.06
Number of mixed male and female alicoles	−.05
Days to pollen	−.03
Total sucker height	.00
Number of double ♀ alicoles on best spike	.00

[a] Coefficients in excess of 0.24 are greater than three times the error.

Two outstanding disherences remain, for which there seems to be no logical interpretation. These are the negative correlation of ramose type with the number of rows in the central spike of the tassel, and the length of the longest tassel branch. A many-rowed central spike clearly is a maize character, and since it is part of the terminal staminate inflorescence which showed no obvious signs of sterility in the group of ramose plants, there is no morphological explanation of the rather high negative correlation. The same is true also of the negative correlation with the length of the longest tassel branch, for which no explanation can be offered.

The two negative coefficients with length of best inflorescence, and the positive correlations with days pollen to silk, are all coherences expected on the hypothesis that the ramose variation is correlated with maize characters. None of the other characters listed have significant coefficients, but it is of interest to compare this series of relationships with those shown for the crinkly variation in Tables IV and V.

The absence of correlation between the ramose type and the number of rows of alicoles on the best spike seems worthy of note. Thus it seems clear from this hybrid that the ramose parent introduced the necessary factors for the production of normal unbranched ears quite independently of the branched character of the inflorescence, and, as a consequence, unbranched inflorescences were obtained closely resembling normal maize ears.

BRACHYTIC × TEOSINTE

Brachytic is a dwarf variation of maize in which the length but not the number of internodes is reduced, and all other organs remain full-sized. In crosses with plants of normal stature this type of dwarf behaves as a simple Mendelian character recessive to the normal form, reappearing in approximately 25 per cent of the F_2 plants, apparently unaltered as to stature (*11*).

Only one F_1 plant was obtained of the hybrid with teosinte, and from this self-pollinated plant a second generation of 290 plants was grown. Of these plants only 35, or 12.1 ± 1.3 per cent were classed as brachytic, a departure from the expected 25 per cent, and too significant to be ascribed to chance. One of these plants is shown in Plate 6. While in many maize crosses the percentage of brachytic plants recovered in the F_2, like that in the case of most recessive characters, is below the expected, the departures usually are within four times the error. The percentage obtained in the teosinte hybrid is not referable readily to the interaction of two independent factors, since it lies midway between the 6.25 per cent expected where the character only appears when two recessive factors are homozygous, and the 18.75 per cent expected in cases where the character appears on the interaction of a dominant and a recessive factor.

Not only is the number of brachytic plants too low for a simple recessive character, but the distinction between normal and brachytic plants is not as clear as in crosses with normal maize. This difference between the maize and the teosinte hybrids is shown by a comparison of the graphs in figures 76 and 83. The failure to obtain definite segregation probably accounts in a large measure for the low number of brachytic plants, and perhaps is due to the introduction of modifying factors through the teosinte parent.

Two plants were found that had brachytic internodes on the lower half and normal internodes above, and one plant was found with a brachytic main stalk and normal suckers. Such instances are not unique nor confined to the hybrid with teosinte, similar plants having been found in maize hybrids after repeated back crossing of brachytic with normal plants.

All varieties of maize exhibit what may be construed as an indication of brachysm, and it is possible to view the origin of the brachytic variation as an example of homeosis, or the transfer of the shortened internodes of the ear stalk to those of the main culm.

In teosinte there is no such indication of brachysm, all branches having elongated internodes. The first indication of the contamination of teosinte with maize is in the direction of brachysm, as instanced by a shortening of the pistillate rachis, resulting in displacing the alignment of the seeds and a shortening also of the lateral vegetative branches.

The absence in teosinte of the hereditary factors that control the shortening of the internodes and their homologues in the lateral inflorescences of maize may be responsible for the failure of simple segregation in the F_2.

CHARACTERS MEASURED

Several characters not recorded in the crinkly and ramose teosinte hybrids were studied in the brachytic hybrid, while other characters used in the former hybrids were not considered. The added characters are: (*a*) Diameter of stalk; (*b*) average length of internodes on best inflorescence; (*c*) rank of pistillate inflorescence.

DIAMETER OF STALK.—This measurement is taken at the smallest place of the largest internode and is recorded in millimeters. In teosinte the average diameter of the stalk is about 2 cm., while in brachytic maize it averages about 4 cm.

AVERAGE LENGTH OF INTERNODES ON BEST INFLORESCENCE.—This measurement is designed to determine whether the brachytic nature of suckers is retained on the lateral branches borne above the ground. The length of the branch in centimeters is divided by the number of internodes. The internodes of teosinte branches usually exceed 10 cm. in length, and in brachytic maize seldom exceed 1 cm.

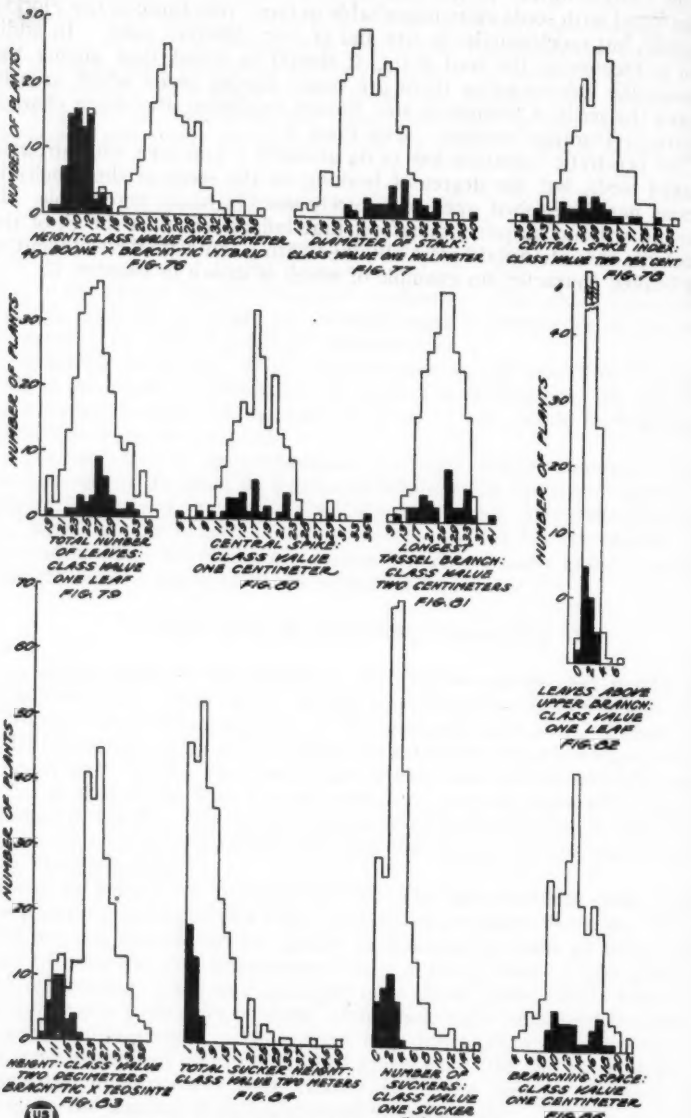
INHERITANCE OF MEASURED CHARACTERS

An examination of the frequency distribution shows that height of plant is the only characteristic having a bimodal distribution which can be attributed to the segregation of the brachytic character. Other bimodal characters are found, but these are not the result of the segregation of brachysm. Unlike the case of the crinkly and ramose hybrids, and similar to that of the Tom Thumb hybrid, no proterogynous plants were obtained in the F_2. The mean number of days from pollen to silk was 5.52 ± 0.13, which is very much less than the 18.3 ± 0.59 observed in the Tom Thumb hybrid.

RANK OF PISTILLATE INFLORESCENCE.—The best pistillate spike from each plant was arranged in a series grading from teosinte to maize. This series was continuous, but for facility in handling the data an effort was made to combine the inflorescences into a few grades. Eight grades were established, grade one including only those spikes which were indistinguishable from pure teosinte, while grade eight embraced the most maizelike inflorescences. There were only four spikes of grade eight, and these resembled poorly developed maize ears. In the intermediate groups the inflorescences were classed as to the number of rows of spikelets, the amount of articulation of the rachis, etc. A fairly normal frequency distribution was obtained for these eight grades, which may be considered as indicating that this grouping of the inflorescences was a natural one. In all other maize-teosinte hybrids in which the Florida strain of teosinte has been used, the seeds of the most teosintelike inflorescences recovered in the F_2 resembled the triangular seeds of the

Durango strain; none were obtained with the trapezoidal seeds typica of the Florida form. In the brachytic hybrid, however, several plants were found with seeds indistinguishable in form from those of the Florida teosinte, but much smaller in size and of very different color. In addition to recovering the seed shape, it should be noted that among the teosintelike inflorescences there are many having seeds which greatly exceed the seeds of teosinte in size, though exhibiting the shape characteristic of Durango teosinte. (See Plate 8.)

The brachytic variation has in its ancestry a pop corn with strongly beaked seeds, but the degree of beaking on the seeds of the brachytic strains has diminished until only rarely are the beaks perceptible. It was not without surprise, therefore, that inflorescences in the F_2 of the brachytic-teosinte hybrid were obtained with a fantastic development of the beaked character, an example of which is shown in Plate 7, C.


NUMBER OF PLANTS
HEIGHT: CLASS VALUE ONE DECIMETER. BOONE X BRACHYTIC HYBRID
FIG. 76
DIAMETER OF STALK: CLASS VALUE ONE MILLIMETER
FIG. 77
CENTRAL SPIKE INDEX: CLASS VALUE TWO PER CENT
FIG. 78
TOTAL NUMBER OF LEAVES: CLASS VALUE ONE LEAF
FIG. 79
CENTRAL SPIKE: CLASS VALUE ONE CENTIMETER
FIG. 80
LONGEST TASSEL BRANCH: CLASS VALUE TWO CENTIMETERS
FIG. 81
LEAVES ABOVE UPPER BRANCH: CLASS VALUE ONE LEAF
FIG. 82
HEIGHT: CLASS VALUE TWO DECIMETERS BRACHYTIC X TEOSINTE
FIG. 83
TOTAL SUCKER HEIGHT: CLASS VALUE TWO METERS
FIG. 84
NUMBER OF SUCKERS: CLASS VALUE ONE SUCKER
FIG. 85
BRANCHING SPACE: CLASS VALUE ONE CENTIMETER
FIG. 86

FREQUENCY DISTRIBUTION OF PLANTS IN F_2
SHADED PORTION REPRESENTS PLANTS CLASSED AS BRACHYTIC

FIGURES 76 TO 86

FIG. 76.—Height; frequency distribution of plants in the F_2 of a Boone×brachytic hybrid. Class value, 1 decimeter. Shaded portion represents plants classed as brachytic.

FIG. 77.—Diameter of stalk; frequency distribution of plants in F_2. Class value, 1 mm. Shaded portion represents plants classed as brachytic.

FIG. 78.—Central spike index; frequency distribution of plants in F_2. Class value, 2 per cent. Shaded portion represents plants classed as brachytic.

FIG. 79.—Total number of leaves; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as brachytic.

FIG. 80.—Central spike; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as brachytic.

FIG. 81.—Longest tassel branch; frequency distribution of plants in F_2. Class value 2 cm. Shaded portion represents plants classed as brachytic.

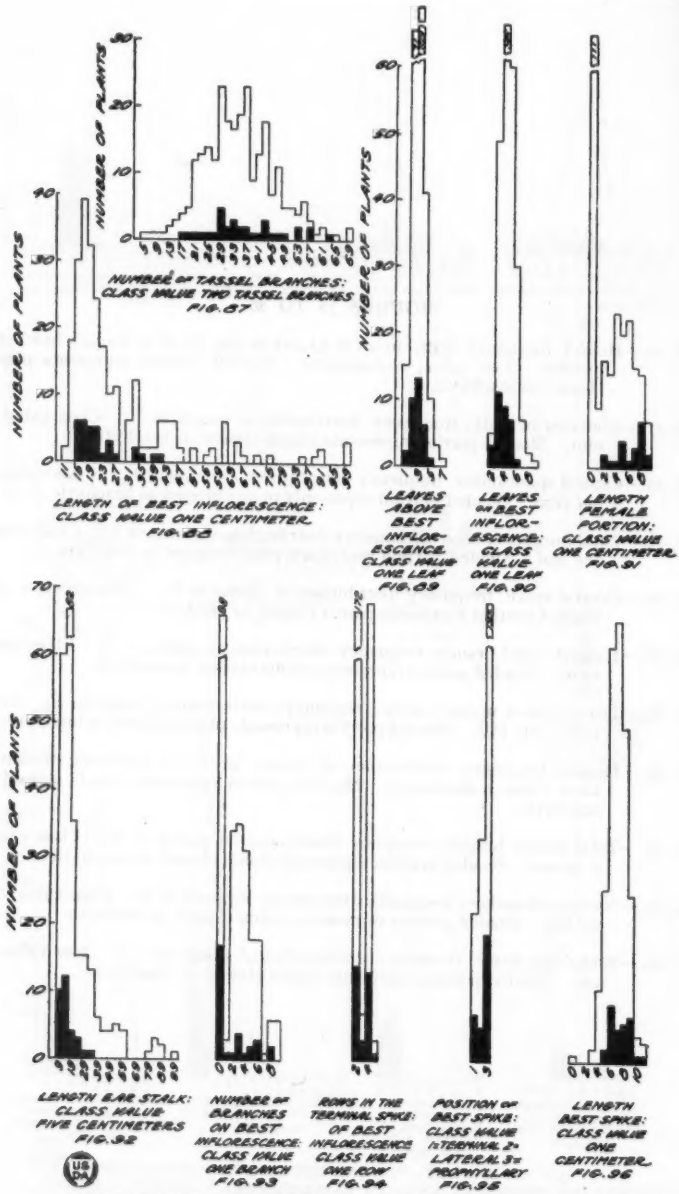
FIG. 82.—Leaves above upper branch; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as brachytic.

FIG. 83.—Height; frequency distribution of plants in F_2 of brachytic×teosinte. Class value 2 decimeters. Shaded portion represents plants classed as brachytic.

FIG. 84.—Total sucker height; frequency distribution of plants in F_2. Class value, 2 meters. Shaded portion represents plants classed as brachytic.

FIG. 85.—Number of suckers; frequency distribution of plants in F_2. Class value, one sucker. Shaded portion represents plants classed as brachytic.

FIG. 86.—Branching space; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as brachytic.


NUMBER OF PLANTS
NUMBER OF TASSEL BRANCHES: CLASS VALUE TWO TASSEL BRANCHES FIG. 87
LENGTH OF BEST INFLORESCENCE: CLASS VALUE ONE CENTIMETER FIG. 88
LEAVES ABOVE BEST INFLORESCENCE: CLASS VALUE ONE LEAF FIG. 89
LEAVES ON BEST INFLORESCENCE: CLASS VALUE ONE LEAF FIG. 90
LENGTH FEMALE PORTION: CLASS VALUE ONE CENTIMETER FIG. 91
LENGTH EAR STALK: CLASS VALUE FIVE CENTIMETERS FIG. 92
NUMBER OF BRANCHES ON BEST INFLORESCENCE: CLASS VALUE ONE BRANCH FIG. 93
ROWS IN THE TERMINAL SPIKE: OF BEST INFLORESCENCE: CLASS VALUE ONE ROW FIG. 94
POSITION OF BEST SPIKE: CLASS VALUE 1=TERMINAL 2= LATERAL 3= PROPHYLLARY FIG. 95
LENGTH BEST SPIKE: CLASS VALUE ONE CENTIMETER FIG. 96

FREQUENCY DISTRIBUTION OF PLANTS IN F_2
SHADED PORTION REPRESENTS PLANTS CLASSED AS BRACHYTIC

FIGURES 87 TO 96

FIG. 87.—Number of tassel branches; frequency distribution of plants in F_2. Class value, two tassel branches. Shaded portion represents plants classed as brachytic.

FIG. 88.—Length of best inflorescence; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as brachytic.

FIG. 89.—Leaves above best inflorescence; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as brachytic.

FIG. 90.—Leaves on best inflorescence; frequency distribution of plants in F_2. Class value, one leaf. Shaded portion represents plants classed as brachytic.

FIG. 91.—Length of female portion of best inflorescence; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as brachytic.

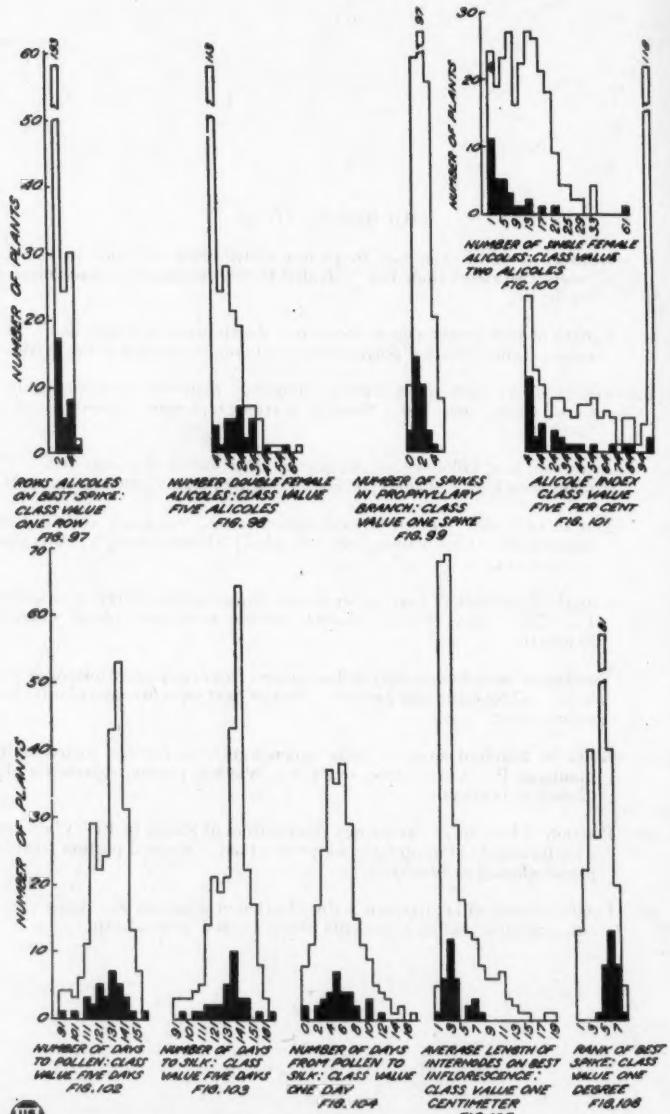
FIG. 92.—Length of ear stalk of best inflorescence; frequency distribution of plants in F_2. Class value, 5 cm. Shaded portion represents plants classed as brachytic.

FIG. 93.—Number of branches on best inflorescence; frequency distribution of plants in F_2. Class value, one branch. Shaded portion represents plants classed as brachytic.

FIG. 94.—Rows in terminal spike of best inflorescence; frequency distribution of plants in F_2. Class value, one row. Shaded portion represents plants classed as brachytic.

FIG. 95.—Position of best spike; frequency distribution of plants in F_2. Class value, 1 for terminal, 2 for lateral, 3 for prophyllary. Shaded portion represents plants classed as brachytic.

FIG. 96.—Length of best spike; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as brachytic.


NUMBER OF PLANTS
ROWS ALICOLES ON BEST SPIKE: CLASS VALUE ONE ROW
FIG. 97
NUMBER DOUBLE FEMALE ALICOLES: CLASS VALUE FIVE ALICOLES
FIG. 98
NUMBER OF SPIKES IN PROPHYLLARY BRANCH: CLASS VALUE ONE SPIKE
FIG. 99
NUMBER OF SINGLE FEMALE ALICOLES: CLASS VALUE TWO ALICOLES
FIG. 100
ALICOLE INDEX CLASS VALUE FIVE PER CENT
FIG. 101
NUMBER OF DAYS TO POLLEN: CLASS VALUE FIVE DAYS
FIG. 102
NUMBER OF DAYS TO SILK: CLASS VALUE FIVE DAYS
FIG. 103
NUMBER OF DAYS FROM POLLEN TO SILK: CLASS VALUE ONE DAY
FIG. 104
AVERAGE LENGTH OF INTERNODES ON BEST INFLORESCENCE: CLASS VALUE ONE CENTIMETER
FIG. 106
RANK OF BEST SPIKE: CLASS VALUE ONE DEGREE
FIG. 108

FREQUENCY DISTRIBUTION OF PLANTS IN F_2
SHADED PORTION REPRESENTS PLANTS CLASSED AS BRACHYTIC

FIGURES 97 TO 106

FIG. 97.—Rows of alicoles on best spike; frequency distribution of plants in F_2. Class value, one row. Shaded portion represents plants classed as brachytic.

FIG. 98.—Number of double female alicoles; frequency distribution of plants in F_2. Class value, five alicoles. Shaded portion represents plants classed as brachytic.

FIG. 99.—Number of spikes in prophyllary branch; frequency distribution of plants in F_2. Class value, one spike. Shaded portion represents plants classed as brachytic.

FIG. 100.—Number of single female alicoles; frequency distribution of plants in F_2. Class value, two alicoles. Shaded portion represents plants classed as brachytic.

FIG. 101.—Alicole index; frequency distribution of plants in F_2. Class value, 5 per cent. Shaded portion represents plants classed as brachytic.

FIG. 102.—Number of days to pollen; frequency distribution of plants in F_2. Class value, 5 days. Shaded portion represents plants classed as brachytic.

FIG. 103.—Number of days to silk; frequency distribution of plants in F_2. Class value, 5 days. Shaded portion represents plants classed as brachytic.

FIG. 104.—Number of days from pollen to silk; frequency distribution of plants in F_2. Class value, 1 day. Shaded portion represents plants classed as brachytic.

FIG. 105.—Average length of internodes on best inflorescence; frequency distribution of plants in F_2. Class value, 1 cm. Shaded portion represents plants classed as brachytic.

FIG. 106.—Rank of best spike; frequency distribution of plants in F_2. Class value, one degree. Shaded portion represents plants classed as brachytic.

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The biometrical constants for the characters considered are given in Table VIII, and the frequency distributions are shown in figures 77–106. In each graph the shaded portion represents the plants classed as brachytic.

CORRELATION OF THE BRACHYTIC VARIATION WITH CHARACTERS OF MAIZE

When the biserial correlations with type of plant are examined it is found that there are 17 coefficients in excess of 3 times the error, while 13 are below this figure (Table IX). Of the 17, height and total sucker height should be eliminated, since these obviously are but other measures of the brachytic nature of the plants. Of the 15 remaining coefficients, 13 are coherences representing a tendency for the brachytic type of plant to reappear in the F_2 accompanied by other maize characters. The two disherences are the negative correlations of brachytic type with central spike index and with the number of leaves on the best inflorescence. Thus the brachytic plants, which usually have central spikes longer than those of normal maize plants and very much longer than those of teosinte plants, are found in this second generation to have relatively short central spikes. The coefficient, however, is only slightly in excess of 3.5 times the error, and may be due to chance. The negative correlation with the number of leaves on the best inflorescence seems incapable of a logical explanation, and must stand as a definite disherence.

TABLE VIII.—*Biometrical constants for the second generation of the brachytic × teosinte hybrid*

Character.	Entire population.			Brachytic group.			Normal group.			Difference.			Fig. number of frequency polygon.
	Mean.	σ	P. E.	Mean.	σ	P. E.	Mean.	σ	P. E.	Amount.	P. E.	Amount. / P. E.	
Height	22. 75	6. 94	0. 278	11. 74	2. 71	0. 309	24. 29	5. 89	0. 253	12. 55	0. 399	31. 48	85
Total sucker height	7. 04	6. 50	. 260	1. 70	1. 35	. 154	7. 77	6. 62	. 278	6. 03	. 318	18. 95	84
Number of suckers	3. 26	2. 49	. 100	1. 60	1. 10	. 125	3. 49	2. 54	. 107	1. 89	. 165	11. 21	85
Diameter of culm	23. 56	4. 24	. 170	27. 91	4. 33	. 494	22. 96	3. 87	. 162	−4. 95	. 520	9. 52	77
Leaves above upper branch	1. 73	. 86	. 034	1. 56	. 82	. 098	1. 73	. 87	. 037	. 19	. 105	1. 81	81
Total number of leaves	26. 44	3. 36	. 134	27. 06	2. 82	. 327	26. 35	3. 44	. 149	. 71	. 358	1. 98	79
Central spike index	58. 61	7. 82	. 352	55. 59	9. 31	1. 108	59. 14	7. 38	. 369	3. 55	1. 167	3. 04	78
Length of branching space	12. 59	3. 33	. 140	13. 03	2. 99	. 353	12. 53	3. 37	. 152	. 50	. 384	1. 30	86
Length of central spike	17. 58	4. 13	. 186	17. 09	5. 68	. 676	17. 67	3. 79	. 190	. 58	. 701	. 83	80
Number of tassel branches	34. 27	11. 25	. 472	36. 27	11. 36	1. 340	33. 97	11. 22	. 505	−2. 30	1. 432	1. 61	87
Length of longest tassel branch	24. 15	5. 34	. 230	24. 79	6. 67	. 787	24. 05	5. 07	. 233	−. 74	. 820	. 92	81
Leaves above best inflorescence	2. 89	1. 00	. 043	2. 81	. 92	. 109	2. 90	1. 02	. 047	. 09	. 119	. 75	89
Leaves on best inflorescence	4. 38	1. 15	. 049	3. 74	1. 02	. 123	4. 47	1. 15	. 053	. 73	. 134	5. 45	90
Length of best inflorescence	26. 53	17. 15	. 737	21. 34	7. 08	. 842	27. 28	18. 05	. 830	5. 94	1. 182	5. 02	88
Length of ear stalk of best inflorescence	19. 38	16. 00	. 688	13. 23	5. 96	. 721	20. 26	16. 83	. 774	7. 03	1. 058	6. 64	92
Length of ♀ portion of best inflorescence	2. 75	2. 94	. 126	4. 26	3. 32	. 402	2. 53	2. 82	. 130	−1. 73	. 423	4. 09	91
Number of branches on best inflorescence	2. 43	2. 44	. 105	2. 03	2. 63	. 318	2. 48	2. 42	. 111	. 45	. 336	1. 34	93

TABLE VIII.—*Biometrical constants for the second generation of the brachytic × teosinte hybrid*—Continued

Character.	Entire population.			Brachytic group.			Normal group.			Difference.			Fig. number of frequency polygon.
	Mean.	σ	P. E.	Mean.	σ	P. E.	Mean.	σ	P. E.	Amount.	P. E.	Amount. P. E.	
Rows in terminal spike of best inflorescence	2. 61	0. 92	0. 040	3. 03	1. 00	0. 121	2. 55	0. 90	0. 041	−0. 48	0. 138	3. 75	94
Position of best spike	2. 69	. 62	. 027	2. 39	. 83	. 100	2. 74	. 55	. 025	. 35	. 103	3. 40	95
Length of best spike	6. 85	1. 51	. 065	7. 45	1. 50	. 182	6. 76	1. 52	. 070	−. 69	. 195	3. 54	96
Number rows of alicoles on best spike	2. 36	. 72	. 031	2. 77	. 94	. 114	2. 30	. 67	. 031	−. 47	. 119	3. 95	97
Number of double ♀ alicoles on best spike	8. 76	11. 78	. 506	20. 13	11. 90	1. 440	7. 14	10. 80	. 497	−12.99	1. 524	8. 52	98
Number of single ♀ alicoles on best spike	10. 99	7. 78	. 334	6. 13	11. 06	1. 338	11. 68	6. 94	. 319	5. 55	1. 375	4. 04	100
Number of spikes in prophyllum	2. 16	1. 09	. 047	1. 52	. 91	. 110	2. 25	1. 10	. 051	. 73	1. 106	. 66	99
Alicole index	64. 47	38. 24	1. 644	24. 32	30. 10	3. 640	70. 17	35. 78	1. 646	45. 85	3. 998	11. 47	101
Days to pollen	126. 85	12. 96	. 544	125. 06	12. 97	1. 543	127. 13	12. 93	. 595	2. 07	. 654	3. 16	102
Days to silk	132. 43	13. 62	. 572	130. 50	13. 58	1. 616	132. 71	13. 58	. 625	2. 21	1. 733	1. 28	103
Days pollen to silk	5. 52	3. 01	. 126	5. 44	2. 74	. 326	5. 53	3. 05	. 140	. 09	. 354	. 25	104
Average length of internodes	4. 40	3. 07	. 132	3. 68	1. 73	. 209	4. 50	3. 20	. 147	. 820	. 256	3. 20	105
Rank of pistillate inflorescence	4. 48	1. 67	. 072	6. 00	. 88	. 106	4. 26	1. 63	. 075	−1. 74	1. 634	1. 07	106

TABLE IX.—*Biserial correlations of brachytic culms with the characters named* [a]

Character.	Correlation.
Height	−0.95±0.03
Alicole index	− .63± .05
Diameter of stalk	.62± .05
Number of double ♀ alicoles	.58± .05
Rank of pistillate inflorescence	.56± .06
Total sucker height	− .55± .05
Number of suckers	− .40± .05
Number of single ♀ alicoles	− .37± .06
Number of spikes in prophyllary	− .35± .07
Rows of alicoles on best spike	.34± .07
Leaves on best inflorescence	− .34± .06
Length of ♀ portion of best spike	.31± .07
Position of best spike	− .29± .07
Rows in terminal spike of best inflorescence	.28± .07
Central spike index	− .25± .07
Length of best spike	.24± .07
Length of ear stalk best inflorescence	− .23± .07
Length of best inflorescence	− .19± .07
Average length of internodes on best inflorescence	.14± .07
Leaves above branch	− .12± .07
Total number of leaves	.11± .07
Number of tassel branches	.11± .07
Number of branches on best inflorescence	− .10± .07
Days to pollen	− .09± .07
Days to silk	− .09± .07
Branching space	.08± .07
Central spike	− .08± .07
Length of longest tassel branch	.07± .07
Leaves above best inflorescence	− .05± .07
Days pollen to silk	− .02± .07

[a] Correlations in excess of 0. 22 are greater than three times the error.

CORRELATION AMONG THE CHARACTERS OF THE PLANTS OF THE F_2

The coefficients of correlation among all the characters of the plants of the second generation are given in Table X. Of these, the most interesting are those of negative sign, since they represent the cases where large dimension of one character is associated with a small dimension in the other. In most such cases the interaction of physiological factors is eliminated, though there are several coefficients of negative sign which are purely mathematical in origin. Thus, the central spike index is of necessity negatively correlated with the length of the branching space, since the index represents the quotient obtained by dividing the length of the central spike by the sum of the length of the organ and the length of the branching space. There are others of a similar nature, but, considering the mass of coefficients in the table, they form a very small percentage.

HEIGHT AND TOTAL SUCKER HEIGHT.—There are three significant disherences with height of plant, and two with total sucker height; but all of these can be discounted for physiological reasons. The nonlinearity of the regression in the correlation involving height tends to reduce the coefficients, so that many of the coefficients not now in excess of three times the error probably are significant. It is worthy of note that with several characters, such as length of the pistillate portion of the best inflorescence and the number of double female alicoles, where physiological and genetic factors are operating in opposite directions, the genetic relationships are strong enough to bring about negative correlations.

TABLE X.—*Coefficients of correlation among the characters of the plants of the second generation of the hybrid between brachytic maize and Florida teosinte*[a]

Character.	Height.	Total sucker height.	Number of suckers.	Diameter of culm.	Leaves above.	Total number of leaves.	Central spike index.	Length of branching space.	Length of central spike.	Number of tassel branches.	Length of longest tassel branch.	Leaves above best inflorescence.	Leaves on best inflorescence.	Length of best inflorescence.	Length of ear stalk of best inflorescence.
Height	.....	.678	.474	D .010	−.014	.327	D .032	.167	D .219	.187	D .173	D .095	D .164	.337	.363
Total sucker height	.678	.....	.915	D .176	−.130	.425	D .010	.148	D .192	.232	D .084	D .045	D .122	.272	.316
Number of suckers	.474	.915	.....	D .105	−.126	.337	D .078	.032	D .134	.148	D .010	D .014	D .090	.142	.200
Diameter of culm	D .010	D .176	D .105	.....	−.095	D .536	D−.214	D .427	.228	D .426	.350	.045	.142	D .243	D .217
Leaves above	−.014	−.130	−.126	−.095	.....	−.130	.045	−.010	.045	−.084	.031	.550	.232	−.032	−.045
Total number of leaves	.327	.425	.337	D .536	−.130	.....	−.152	D−.148	.032	.331	−.010	D .123	−.063	.148	.138
Central spike index	D .032	D .010	D .078	D−.214	.045	−.152	.....	−.603	.535	−.445	.045	D−.084	D−.078	−.148	−.110
Length of branching space	.167	.148	.032	D .427	−.010	D−.148	−.603	.....	D .226	.592	.474	D .032	D .349	.383	.350
Length of central spike	D .219	D .192	D .134	.228	.045	−.032	.535	D .226	.....	D .055	.610	D−.078	.286	D .215	D .228
Number of tassel branches	.187	.232	.148	D .426	−.084	.331	−.445	.592	D .055	.....	D .313	D .090	D .219	.368	.380
Length of longest tassel branch	D .173	D .084	D .010	.350	.032	−.010	.045	D .474	.610	D .313	.....	D−.063	.243	D .236	D .230
Leaves above best inflorescence	D .095	D .045	D .014	.045	.556	D .123	D−.084	D .032	D−.078	D .090	D−.063	.....	.264	D .161	D .126
Leaves on best inflorescence	D .164	D .122	D .090	.142	.232	−.063	D−.078	D .349	.286	D .219	.243	.264	.....	D .319	D .298
Length of best inflorescence	.337	.272	.142	D .243	−.032	.148	−.148	.383	D .215	.368	D .236	D .161	D .319	.....	.952
Length of ear stalk of best inflorescence	.363	.316	.200	D .217	−.045	.138	−.110	.350	D .228	.380	D .230	D .126	D .298	.952	.....
Length of ♀ portion of best inflorescence	−.281	−.314	−.284	D−.055	.219	−.182	.071	−.138	D−.045	−.279	D−.032	.078	D−.105	−.448	−.446
Number of branches on best inflorescence	.232	.268	.210	D .295	−.176	.277	−.210	.346	D .100	.510	D .179	D .014	D .126	.570	.553
Rows in terminal spike of best inflorescence	−.182	−.084	−.078	.158	.032	−.138	D−.010	D .055	.100	−.063	.071	D−.090	.055	−.179	−.176
Position of best spike	.184	.195	.167	D .001	−.078	.017	−.078	.182	D .063	.118	D .090	−.095	D .017	.167	.167
Length of best spike	−.045	−.045	−.078	.319	.138	.084	D−.110	D .237	.100	D .032	.184	.100	.010	D .045	−.003
Rows of alicoles on best spike	−.290	−.190	−.202	.197	.032	−.032	D−.118	D .084	.005	D .078	.020	.055	.158	−.045	−.055
Number of double ♀ alicoles on best spike	−.365	−.337	−.343	.219	.184	−.118	D−.197	D .274	.090	D .045	.114	.095	.118	−.010	−.055
Number of single ♀ alicoles on best spike	.214	.253	.239	D .020	−.100	.100	D .130	D−.084	D .045	.032	D .055	−.017	D .055	.063	.078
Number of spikes in prophyllum	.363	.283	.207	D .032	D .063	.017	D .032	.167	D .205	.084	D .184	−.045	D .110	.390	.393
Alicole index[b]	.349	.353	.356	−.133	−.119	.086	D .093	−.113	−.094	D−.143	−.309	−.027	D−.206	D−.053	D−.039
Days to pollen	.195	.155	.126	D .138	−.200	.587	D .014	D−.158	−.179	.078	−.142	−.032	−.202	D−.105	D−.090
Days to silk	.185	.138	.110	D .126	−.200	.554	D .022	D−.118	−.134	.105	−.100	−.045	−.152	D−.084	D−.063
Days pollen to silk	D .006	−.032	−.032	D−.006	D−.063	D .014	.032	D .095	.144	D .144	.148	D−.071	.161	D .055	D .071
Average length of internodes	.305	.263	.155	D .197	−.118	.170	−.114	.268	D .126	.355	D .148	D .032	−.055	.861	.908
Rank of pistillate inflorescence	−.398	−.362	−.349	.164	.176	−.219	D−.010	.173	.187	D .032	.158	D−.045	.202	−.032	−.078

[a] Coefficients preceded by the letter "D" are those in which characters derived from different parents tend to remain associated. Coefficients in excess of 0.145 exceed three times their error.

[b] Biserial correlations. Coefficients in excess of 0.184 are greater than three times their error.

TABLE X.—*Coefficients of correlation among the characters of the plants of the second generation of the hybrid between brachytic maize and Florida teosinte*—Continued

Character.	Length of ♀ portion of best inflorescence.	Number of branches on best inflorescence.	Rows in terminal spike of best inflorescence.	Position of best spike.	Length of best spike.	Rows of alicoles on best spike.	Number of double ♀ alicoles on best spike.	Number of single ♀ alicoles on best spike.	Number of spikes in prophyllum.	Alicole index.	Days to pollen.	Days to silk.	Days pollen to silk.	Average length of internodes.	Rank of pistillate inflorescence.
Height	−.281	.232	−.182	.184	−.045	−.290	−.365	.214	.363	.349	.195	.185	D .006	.305	−.398
Total sucker height	−.314	.268	−.084	.195	−.045	−.190	−.337	.253	.283	.353	.155	.138	−.032	.363	−.362
Number of suckers	−.284	.210	−.078	.167	−.078	−.202	−.343	.239	.207	.356	.126	.110	−.032	.155	−.349
Diameter of culm	D−.055	D .295	.158	D .001	.319	.197	.219	D .020	D .032	−.233	D .138	D .126	D−.006	D .197	.164
Leaves above	.219	−.176	.032	−.078	.138	.032	.184	−.100	D .063	−.119	−.200	−.200	D−.063	−.118	.176
Total number of leaves	−.182	.277	−.138	.017	.084	−.032	−.118	.100	.017	.086	.587	.554	D .014	.170	−.219
Central spike index	.071	−.210	D−.010	−.078	D−.110	D−.118	D−.197	D .130	D .032	D .093	D .014	D .022	.032	−.114	D−.010
Length of branching space	−.138	.346	D .055	.182	D .237	D .084	D .274	D−.084	.167	−.113	D−.152	D−.118	D .095	.268	.173
Length of central spike	D−.045	D .100	.100	D .063	.100	.005	.090	D .045	D .205	−.094	−.179	−.134	.144	D .126	.187
Number of tassel branches	−.279	.510	−.063	.118	D .032	D .078	D .045	.032	.084	D−.143	.078	.105	D .144	.355	D .032
Length of longest tassel branch	D−.032	D .179	.071	D .090	.184	.020	.114	D .055	D .184	−.309	−.142	−.100	.148	D .148	.158
Leaves above best inflorescence	.078	D .014	D−.090	−.095	.100	.055	.095	−.017	−.045	−.022	−.032	−.045	D−.071	D .032	D−.045
Leaves on best inflorescence	D−.105	D .126	.055	D .017	.010	.158	.118	D .055	D .110	D−.206	−.202	−.152	.161	−.055	.202
Length of best inflorescence	−.448	.570	−.179	.167	D .045	−.045	−.010	.063	.390	D−.053	D−.105	D−.084	D .055	.861	−.032
Length of ear stalk of best inflorescence	−.466	.553	−.176	.167	−.003	−.055	−.055	.078	.393	D−.039	D−.090	D−.063	D .071	.908	−.078
Length of ♀ portion of best inflorescence	.....	−.629	.431	−.392	.173	.230	.331	−.164	−.235	−.264	−.126	−.148	−.118	−.493	.296
Number of branches on best inflorescence	−.629	.....	−.281	.306	D .014	−.055	−.090	.130	.210	.055	.071	.084	D .090	.568	−.078
Rows in terminal spike of best inflorescence	.431	−.281	.....	−.263	.138	.425	.373	−.105	−.105	−.335	−.274	−.277	D−.095	−.219	.422
Position of best spike	−.392	.306	−.263	.....	D .063	−.364	−.195	.090	.322	.100	D−.078	D−.084	−.071	.197	−.197
Length of best spike	.173	D .014	.138	D .063	.....	.138	.311	D .118	D .045	−.212	−.192	−.185	D−.014	−.005	.148
Rows of alicoles on best spike	.230	−.055	.425	−.364	.138	.....	.466	D .090	−.167	−.200	−.182	−.173	D−.032	−.090	.466
Number of double ♀ alcoles on best spike	.331	−.090	.373	−.195	.311	.466	.....	−.598	−.134	−.883	−.351	−.330	D−.010	−.095	.654
Number of single ♀ alicoles on best spike	−.164	.130	−.105	.090	D .118	D .090	−.598	.....	.105	.660	.126	.110	−.032	.063	−.256
Number of spikes in prophyllum	−.235	.210	−.105	.322	D .045	−.167	−.134	.105	.....	D−.074	D−.173	D−.197	−.152	.395	−.104
Alicole index [b]	−.264	.055	−.335	.100	−.212	−.200	−.883	.660	D−.074	.....	.345	.314	−.012	.056	−.353
Days to pollen	−.126	.071	−.274	D−.078	−.192	−.182	−.351	.126	D−.173	.345	.....	.974	D .167	D−.014	−.404
Days to silk	−.148	.084	−.277	D−.084	−.185	−.173	−.330	.110	D−.197	.314	.974	.....	D .385	D−.010	−.381
Days pollen to silk	−.118	D .090	D−.095	−.071	D−.014	D−.032	D−.010	−.032	−.152	−.012	D .167	D .385	.....	D .017	D−.014
Average length of internodes	−.493	.568	−.219	.197	−.005	−.090	−.095	.063	.395	.056	D−.014	D−.010	D .017	.....	−.142
Rank of pistillate inflorescence	.296	−.078	.422	−.197	.148	.466	.654	−.256	−.104	−.353	−.404	−.381	D−.014	−.142	.....

[b] Biserial correlations. Coefficients in excess of 0.184 are greater than three times their error.

NUMBER OF SUCKERS.—While there are 15 significant correlations with number of suckers, all but four of these would be expected for both physiological and genetic reasons. Of the four which can be explained only on the basis of genetic relationship, the highest is with rank of the pistillate inflorescence, and all involve some measure of the form of this inflorescence. These correlations indicate clearly a tendency for plants with few suckers to bear maizelike inflorescences.

DIAMETER OF CULM.—Normal maize and teosinte differ pronouncedly in diameter of the culm, and this difference is greatly magnified when the maize parent is brachytic; yet, notwithstanding this fact, there are more disherences with diameter of culm in the brachytic-teosinte hybrid than with any of the other characters studied. It seems clear that physiological factors are able to mask most of the genetic relationships which exist, though the negative correlation with alicole index indicates that the most maizelike pistillate inflorescences will occur on plants with the thickest culms.

LEAVES ABOVE UPPER BRANCH.—With leaves above the upper branch, which is one of the best differentiating characters between maize and teosinte, there are no significant disherences. While the coefficients for none of the correlations with this character are high, with the exception of that with the leaves above the best inflorescence, the many negative coefficients where physiological and gentic factors are at work in opposite directions indicate the relative strength of the gentic relationships.

TOTAL NUMBER OF LEAVES.—With the character, "total number of leaves," there are two significant disherences, one of which can not be explained readily on the basis of the interaction of physiological factors; but in this case the coefficient of -0.148 is but slightly in excess of three times the error, and with the number of coefficients under consideration several chance departures of this magnitude from complete independence are to be expected. Of the coherences, there are three clear examples of linkage, those with central spike index, length of the pistillate portion of the best spike, and rank of the pistillate inflorescence.

CENTRAL SPIKE INDEX.—Relatively long central spikes are an outstanding characteristic of brachytic maize, but from the standpoint of correlations with other characters the index is unsatisfactory. While there are only two significant disherences there is a complete absence of clear genetic linkage.

BRANCHING SPACE.—The length of the branching space also is unsatisfactory from the standpoint of correlations, since in many instances physiological and genetic factors operate in the same direction; and where disherences are found they obviously are due to the greater weight of the physiological factors.

LENGTH OF CENTRAL SPIKE.—This character has many of the objections of the other measures of the terminal panicle, though it should be observed that the negative correlations with days to pollen and silk, the former significant, show that linkage is involved with these complex characters.

NUMBER OF TASSEL BRANCHES.—There is one clear genetic relationship with this character, that with the length of the pistillate portion of the best spike, though, curiously enough, this relationship is not sustained with the other measures of the pistillate inflorescence.

LENGTH OF THE LONGEST TASSEL BRANCH.—While there are several significant disherences with this character, all can be ascribed to the interaction of physiological factors. There is one clear genetic correlation evidenced in the negative coefficient of -0.309 with alicole index.

LEAVES ABOVE THE BEST INFLORESCENCE.—With leaves above, where several genetic correlations were anticipated, none was found; and, while there are some unexpected disherences, these can be attributed to physiological causes.

NUMBER OF LEAVES ON THE BEST INFLORESCENCE.—With the number of leaves on the best inflorescence there are no significant correlations indicating disherences which can not be explained on physiological grounds; while the negative correlations with length of season seem clear examples of coherence brought about by genetic factors.

LENGTH OF THE BEST INFLORESCENCE.—With the length of the best inflorescence there are two clear genetic correlations, both negative; that with the rows in the terminal spike of the best inflorescence, and that with the length of the pistillate portion. The former is not large, but the latter is one of the best gentic correlations found. It seems clear that the plants with long branches tend to terminate in staminate rather than pistillate inflorescences, resembling teosinte in this respect.

LENGTH OF EAR STALK OF THE BEST INFLORESCENCE.—With length of ear stalk, which in teosinte is extremely long and in brachytic maize relatively short, essentially the same correlations are found as with the length of the best inflorescence, and, since these two measurements are closely correlated ($r=0.952$), such behavior is a necessary consequence. The high correlation of 0.952 is not unexpected in view of the fact that by far the largest part of the total length of the best inflorescence is made up of the length of the ear stalk, the length of the flowering parts forming only a small part of the whole.

LENGTH OF THE PISTILLATE PORTION OF THE BEST INFLORESCENCE.—With the length of the pistillate portion of the terminal panicle of the best inflorescence there are fourteen coefficients of negative sign which exceed three time the error. These coefficients all indicate genetic correlations, and include such complex characters as height and season. In addition to the negative coefficients, there are several others of positive sign which also represent genetic rather than physiological relationship. It seems worthy of note that there are no significant disherences with this character.

NUMBER OF BRANCHES IN THE TERMINAL PANICLE OF THE BEST INFLORESCENCE.—With the number of branches on the terminal panicle of the best inflorescence there are two significant disherences, but, like so many of the preceding instances of this sort, both are capable of explanation on physiological grounds.

NUMBER OF ROWS IN THE TERMINAL SPIKE OF THE BEST INFLORESCENCE.—With the number of rows in the terminal spike of the best inflorescence there are no significant disherences; there are several rather high correlations with other characters of the flowering parts.

POSITION OF THE BEST SPIKE.—With the position of the best spike there is one outstanding disherence—that with days to pollen. In this case the plants having the best spikes in the axils of the prophylla, as in teosinte, are those with the shorter season. This negative correlation seems contrary to that expected, both genetically and physiologically. There is one outstanding correlation that clearly can be attributed to genetic causes, namely, that of $-.364$ with the rows of alicoles on the best spike.

LENGTH OF BEST SPIKE.—There are several significant genetic correlations with length of best spike, and no disherent correlations which can not be attributed to physiological factors.

NUMBER OF ROWS OF ALICOLES ON BEST SPIKE.—With the number of rows of alicoles on the best spike, which is one of the outstanding differences between maize and Euchlaena, there are no significant disherent correlations. It is interesting to observe that this character is negatively correlated with the measures of height as well as with season.

NUMBER OF DOUBLE FEMALE ALICOLES ON BEST SPIKE.—The number of double female alicoles and the number of single female alicoles, which in a certain sense are two complementary characters, both show significant genetic correlations, and no clear disherences. It seems noteworthy that where the number of double female alicoles is negatively correlated with the measures of height and season, the number of single female alicoles is positively correlated with these characters.

NUMBER OF SPIKES IN PROPHYLLARY.—The number of spikes in the prophyllary inflorescence has four significant correlations which represent disherences, but these all may be due to the interaction of physiological factors. On the other hand, there are several coefficients which can best be attributed to genetic causes.

ALICOLE INDEX.—This index measures the proportion of single female alicoles, which is one of the outstanding differences between maize and teosinte. It is of interest to observe that in this character there is but one significant disherence, and many clear genetic correlations.

DAYS TO POLLEN AND DAYS TO SILK.—With length of season as measured by the number of days from planting to anthesis and silking there are several significant disherences, the most outstanding being those with the number of spikes in the prophyllary inflorescence and the number of days between anthesis and the appearance of the first silk. The negative correlations with the number of spikes in the prophyllary inflorescence are contrary to expectation on both physiological and genetic grounds, while the positive correlations with days from pollen to silk might be attributed to the advancing season, with cool weather retarding the appearance of silking.

DAYS POLLEN TO SILK.—Of the 29 correlations with days from pollen to silk, there are only five in excess of three times the error; of these, two are disherences. The character as a whole does not seem to be a stable one, or one in which much confidence can be placed, though the teosinte parent always is proterogynous and the maize parent proterandrous.

AVERAGE LENGTH OF INTERNODE.—There is one significant disherence with the average length of the internode on the best branch, namely, that with diameter of culm; but since it has been apparent throughout that physiological factors have affected the diameter of the culm to the almost complete exclusion of genetic factors, no importance need be attached to this single disherence.

RANK OF THE PISTILLATE INFLORESCENCE.—The rank of the pistillate inflorescence, where the best spike of each plant was arranged in an ascending series from teosinte to maize, and this series was distributed among eight fairly definite groups, furnishes a composite measure evaluating all the characters of the spike. A fairly normal frequency distribution resulted from the grouping of these spikes, and the rank, therefore, may be taken as a fair estimate of the degree of resemblance of the spike to maize or teosinte. The correlations with rank should indicate to what extent the maizelike form of inflorescence is associated with the other characteristics of maize.

There are 21 significant correlations in a possible 29, and, without exception, these correlations indicate a tendency for the maizelike form of pistillate inflorescence to be associated in inheritance with other characters of maize.

The high correlation of rank with the number of double female alicoles (0.654), rather than with alicole index, arouses the suspicion that size was largely the determining factor in arranging the spikes. However, the correlation of rank with length of spike is only 0.148, and the partial correlation of rank with the number of double female alicoles for constant length of spikes is 0.648 ± 0.028. Mere size, therefore, could not have been an important factor in grading the ears.

Aside from the correlations of the several characteristics of the inflorescences with rank, the correlations with season seem worthy of note. Thus, it is apparent that the maizelike form of inflorescence is found on the earlier plants, a condition to be expected from the interaction of genetic factors.

SUMMARY

Several hybrids between normal maize and teosinte have been grown and, aside from variations in size, the first and second generations of such hybrids are very much alike. These generations are similar in inheritance to the hybrid between Tom Thumb pop corn and Florida teosinte, the inheritance of which has been reported previously.

In view of the seemingly complete blending of characters of both parents in such hybrids, it became of interest to analyze the behavior of some of the more strictly Mendelian variations of maize in hybrids with teosinte.

The present paper reports the inheritance of three striking Mendelian characters of maize, crinkly, ramose, and brachytic, in hybrids with the annual, teosinte, *Euchlaena mexicana*. As in hybrids with normal maize, all three variations are recessive in the hybrid with teosinte, and all three reappeared in the F_2, the two former in the expected monohybrid percentage of 25, but the last in only 12 per cent of the plants.

With the crinkly variation none of the measures of this character showed a bimodal distribution, though it was possible to classify the plants arbitrarily into two groups on their general appearance.

The several characteristics of the crinkly variation were found to be correlated among themselves, though in some cases the degree of correlation was low. The crinkly type of plant, as classed in the field, was found to be associated with maize characters not involved in the change from normal to crinkly, such as the form of the pistillate inflorescence, etc. This behavior indicates that there are genetic correlations among the maize characters in hybrids with teosinte, as well as a correlation between these characters and the mutant type, crinkly.

The classification of ramose plants in the F_2 of the hybrid with teosinte was accomplished without difficulty and, while variation obviously existed among the plants classed as ramose, this was not as pronounced as in the ramose-Gordo hybrid (*12*). The variability was visible chiefly in the tassels, the pistillate inflorescences seeming to be more uniform. Thus, no intermediate pistillate spikes were found, all the ramose spikes being branched along the entire axis.

The teosintelike plants with ramose inflorescences, though apparently functioning normally with respect to the production of male gametes, were practically sterile with respect to the production of female gametes.

Not only were seeds not produced by these plants but spikelets were formed only rarely, the inflorescences usually consisting of naked feathery branches. This sterility, though most pronounced in the group more nearly approximating the teosinte parent with respect to other characters, was apparent also throughout the entire ramose group. Fertile seeds, however, were matured by the ramose plants that were most maizelike with respect to other characters.

Since the ramose form of inflorescence is considered as a reversion to a more primitive and possibly ancestral type, its complete sterility in hybrids with the nearest wild relative of maize may be not without significance. The sterile inflorescences, while not succulent, suggest the sterile cauliflower form found in crosses between ramose and podded strains.

The combination of the teosinte form of pistillate inflorescence with the branched condition of ramose was completely sterile, and there seems to be little reason to believe that such a combination represents an ancestral form.

The ramose form of inflorescence, like the crinkly type of plant, was found to be associated with some of the characters of maize not involved in the change from normal to ramose inflorescences, thus furnishing additional evidence that there is a correlated complex of maize characters which tends to reappear in the perjugate generations of hybrids with teosinte. The ramose form, however, is correlated with only three maize characters, and two instances of apparent disherence are found.

The brachytic segregates of the F_2 teosinte hybrid resembled the normal segregates much more closely than has been found to be the case in brachytic-normal maize hybrids; and there seems little doubt that modifying factors affecting stature have been introduced through the teosinte parent. Only 12 per cent of the plants of the second generation were classified as brachytic.

As in the two preceding characters, brachytic culms are found to be associated with other maize characters; and, while the correlations often are not high, it seems clear that somewhat the same complex of maize characters is involved as in the other two hybrids.

All three characters, crinkly, ramose, and brachytic, are found to be correlated with other characters of maize, but in many cases the characters involved differ in the three hybrids. Thus the crinkly type of plant shows a high correlation with short season, as indicated by the negative coefficients with days to pollen and days to silk, while neither the ramose nor brachytic plants show correlations with season. Similarly, crinkly is associated with few leaves, while the other two characters show no such association. Both crinkly and brachytic plants have few suckers, but the ramose plants seem not to have this limitation.

It seems clear that many of the multiple-factor characters of maize are correlated with these three unit characters, but the characters involved and the degree of closeness of their relations differ in the three hybrids.

The close relationship of maize and teosinte is further emphasized by these hybrids and, with the exception of the ramose type of branching, there is little evidence of incompatible combinations.

On the other hand, the cross with brachytic maize indicates that teosinte possesses modifying factors for this character not present in at least a large number of maize varieties. This same condition was indicated also by the hybrids with golden and rainbow.

It is further shown that the branching of the ramose variation, which would seem to represent a reversion to a more primitive form, does not approximate the branched inflorescence of teosinte, but is farther removed from teosinte than from normal maize.

With respect to the correlations among the characters which differentiate maize and teosinte, but which are not involved in the change from normal maize to the three variations studied, there seems to be practically complete freedom of recombination within the limits of physiological relationships.

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PLATE 1

Lateral inflorescence from a plant of the first generation of a cross between pod corn and teosinte. The husks have been removed to show the character of the spikes. Natural size.

PLATE I

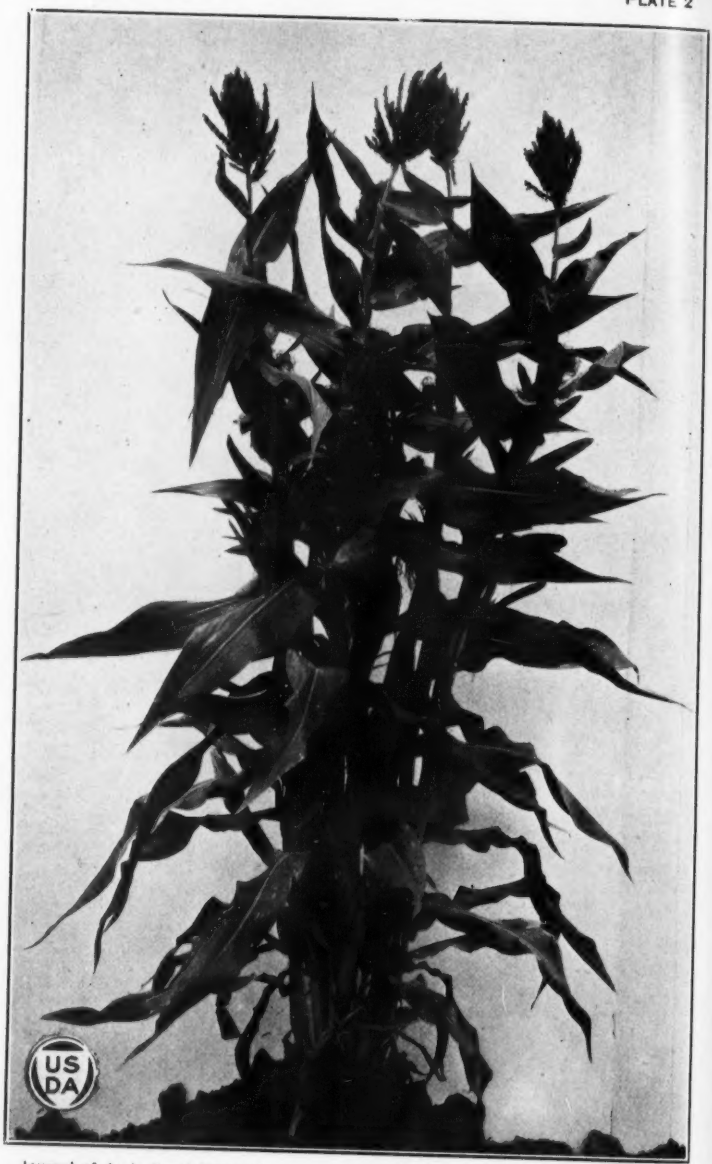

PLATE 2

Plant of the second generation of crinkly maize × teosinte. This plant exhibits many of the characteristics of crinkly maize.

PLATE 3

Plant of the second generation of crinkly maize × teosinte. This plant, in contrast to that shown in Plate 2, exhibits many of the characteristics of teosinte.

PLATE 3

PLATE 4

Terminal inflorescence of the plant represented in Plate 2, showing the compact type of tassel typical of crinkly maize. Natural size.

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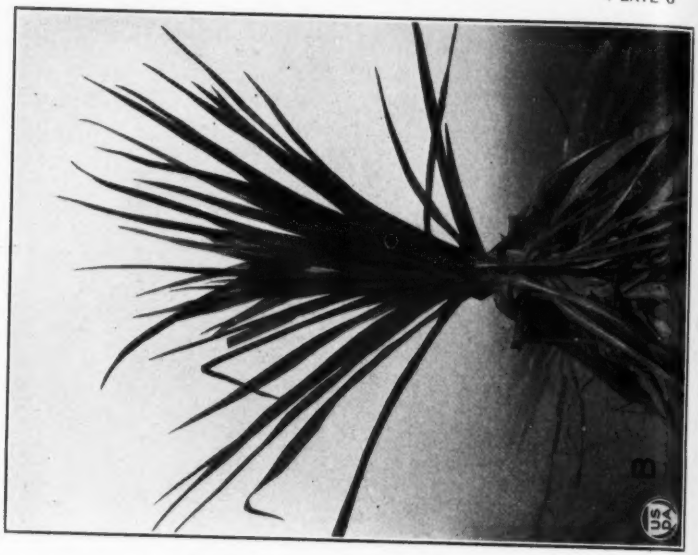
PLATE 5

Section of a leaf from the plant shown in Plate 2 showing pronounced lobing at the base. About natural size.

PLATE 5


B

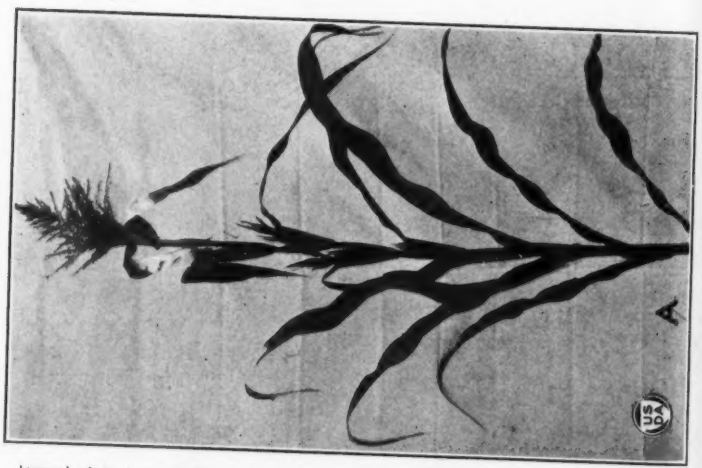

A

PLATE 6

A.—A ramose plant from the second generation of ramose maize × teosinte. Note the typical ramose tassel.

B.—A spike-leaved brachytic plant from the second generation of brachytic maize × teosinte.

PLATE 7

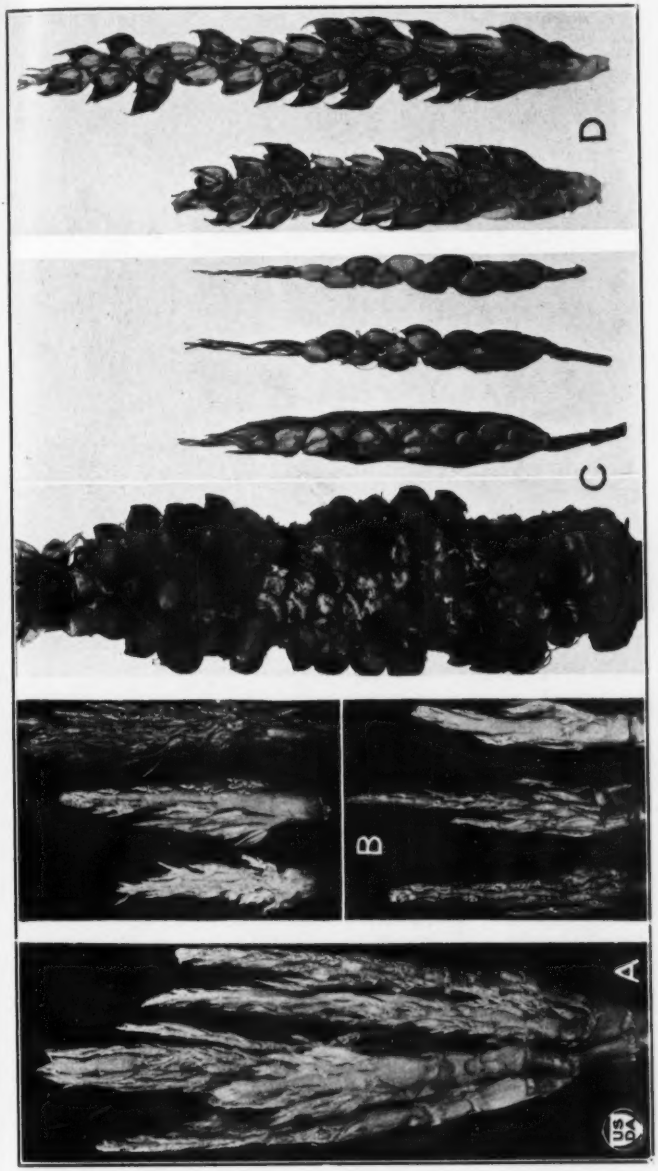
A.—Lateral inflorescence from the plant represented in Plate 6, A. The husks have been removed to show the character of the spikes.

B.—Individual spikes from the prophyllary branch of the inflorescence shown at the left in A.

C.—The most maizelike and most teosintelike inflorescences obtained in the second generation of the ramose maize × teosinte hybrid. The teosintelike seeds resemble the triangular seeds of Durango teosinte rather than the seeds of the Florida teosinte parent. Natural size.

D.—Spikes from the second generation of brachytic maize × teosinte, showing extreme form of beaked seeds. Natural size.

Beaked seeds were a characteristic of one of the great-grandparents of the brachytic maize, but were not noticeable in the immediate brachytic plant which served as the female parent of the brachytic-teosinte hybrid.


D
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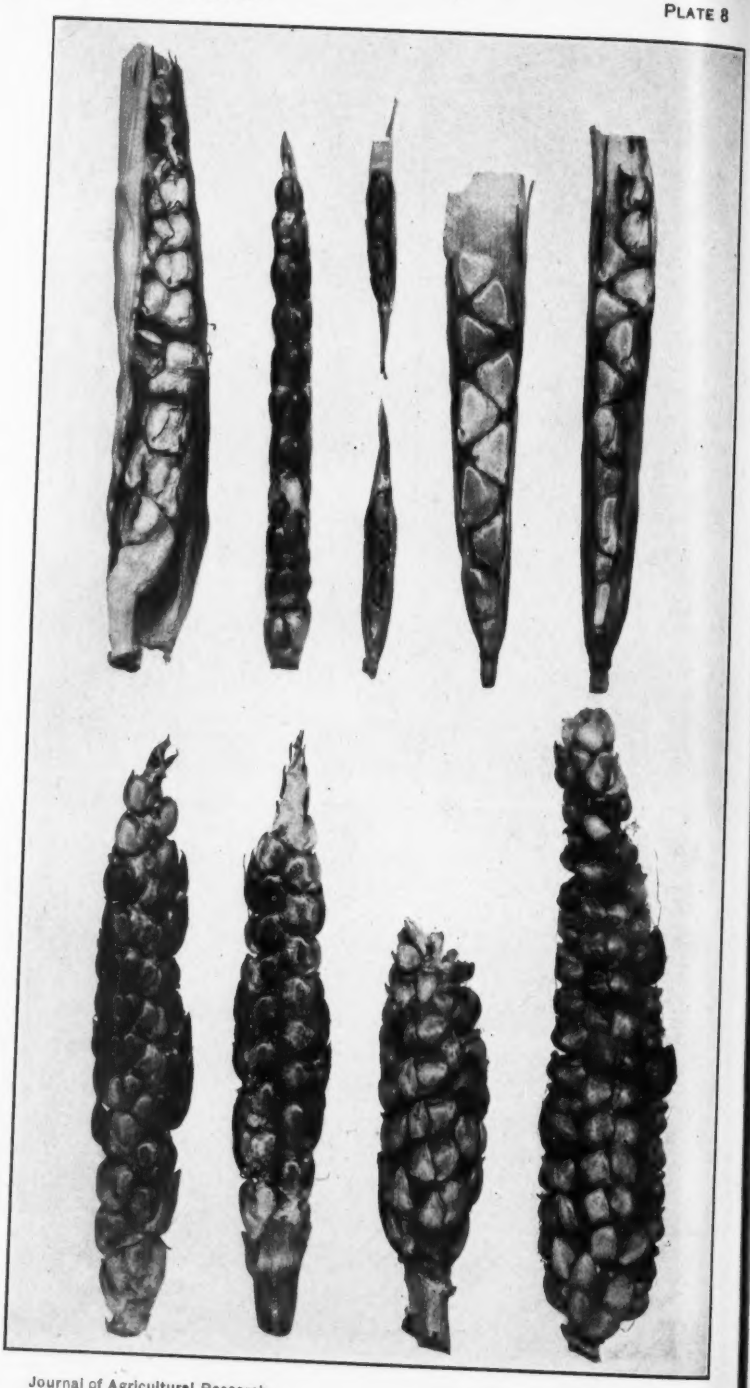
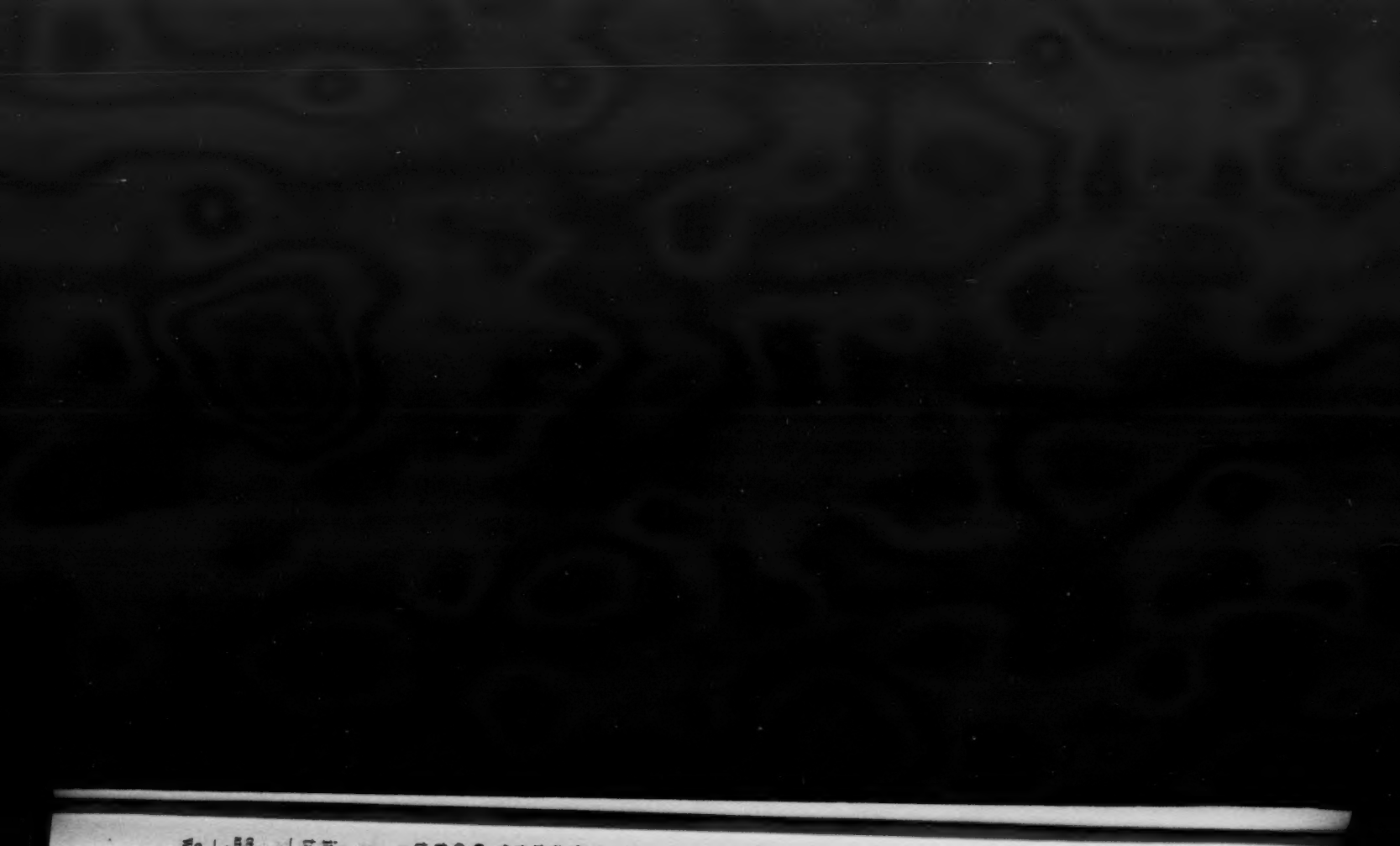


PLATE 8

Spikes from the second generation of brachytic maize × teosinte. The two spikes at the upper right show the gigantic seeds resembling in form Durango teosinte. The two spikes in the upper center are the most teosinte like recovered in maize-teosinte hybrids and have seeds which resemble in form the seeds of the Florida teosinte parent though much smaller in size. The four spikes at the left (2 upper and 2 lower) are from a single plant of the F_2 and represent very closely inflorescences typical of F_1 plants. The upper left-hand spike is terminal and shows the "saddle-back" condition encountered in maize-teosinte crosses.

The two spikes at the lower right are the most maize like inflorescences found in the F_2 of brachytic maize × teosinte.



THE UTILIZATION OF LACTOSE BY THE CHICKEN[1]

By T. S. HAMILTON, *Division of Animal Nutrition*, and L. E. CARD, *Division of Poultry Husbandry, Illinois Agricultural Experiment Station*[2]

The value of milk, in its various forms, as a poultry feed has been clearly established, the high quality of its proteins and minerals being its chief assets. The present investigation was undertaken primarily for the purpose of determining whether or not lactose, the carbohydrate of milk, was utilized by the chicken. It is not always realized that lactose represents approximately 38 per cent of the total solids and approximately 30 per cent of the energy of whole milk, while the total proteins contain but 26 per cent of the solids and approximately 20 per cent of the energy of whole milk. In some commercial milk preparations the percentage of lactose is much higher; whole milk powder contains 34 to 41 per cent, skim milk powder 48 to 54 per cent, and secwa, or dried whey, contains approximately 74.5 per cent lactose and 14.2 per cent soluble albumin (*5*).[3] From a practical point of view the carbohydrates of a ration usually seem of less importance than the protein because of the lower relative cost of the former, but a knowledge of the amount and utilization of the carbohydrates present is necessary in order to formulate the most desirable and economical ration for a particular purpose. Thus a knowledge of the amount and degree of utilization of the lactose in milk is of practical importance to the science of poultry feeding. The question is also of theoretical interest because at no stage in the life of the chicken is milk, or any other substance containing lactose, a part of its natural diet, and therefore the utilization of lactose, which normally requires the presence of a lactase, might rightfully be questioned on teleological grounds.

The literature available on the subject of the utilization of lactose by the fowl is very meager. In addition to investigations on the adaptation of various digestive organs to lactose, only two studies have been found dealing directly with the question. Shaw (*7*), in a study of digestion in the chick, concluded that lactose was not digested and, further, that it acted as an irritant to the gastrointestinal mucosa. Chicks fed from birth on milk alone died on the third day and the contents of no part of the intestinal tract gave a positive test for monosaccharids with Barfoed's reagent. That lactose was present was shown by preparing the phenyllactosazone crystals. Plimmer and Rosedale (*6*), on the other hand, claim to have fed chickens from birth to a period exceeding three months on a diet containing lactose. Failure to find reducing sugars in the excreta was taken to indicate the assimilation of lactose.

EXPERIMENTAL DATA

In determining the utilization of lactose, the reducing sugars present in the excreta of hens fed on an ordinary cereal diet and on a diet containing variable amounts of lactose were estimated. Seven experiments,

[1] Received for publication Jan. 26, 1924.
[2] The writers desire to thank Dr. H. H. Mitchell for many helpful suggestions and advice regarding certain procedures followed in this work. They are also indebted to C. I. Bray for some preliminary analytical work in connection with the sugar methods used.
[3] Reference is made by number (italic) to "Literature cited," p. 604.

each of one week's duration, were made. In all experiments in which lactose was fed, except Experiment No. 2, the hens received the lactose with their mash on each of three successive days. The excreta were collected daily during these three days as well as during the four following days in order to allow sufficient time for the excretion of any unabsorbed lactose. Between successive experiments four days were ordinarily allowed to elapse.

In Experiment No. 2 two grams of lactose were fed daily to each hen for seven days. The excreta were collected on the seventh day only. Four mature White Wyandotte hens were used in this investigation. Each hen was kept in a wire cage 15 inches wide, 24 inches long, and 14 inches high. The wires of the cage were 2 inches apart one way and 4 inches apart the other. In the bottom of the cage was the excreta-collection pan, which was of the same width and length as the cage and 1.5 inches deep. It rested on flat iron grooves which held the pan firmly in place but which permitted removal for cleaning. The pan was made water-tight, of medium weight galvanized iron. Inside of the pan was an iron frame covered with hardware cloth. This frame was just enough smaller than the pan to fit closely within it and was raised about 1 inch from the bottom. The hen stood on this frame and the excreta for the most part soon passed through the hardware cloth into the pan below. In this manner the excreta were neither trampled over nor scratched out and lost. The feeding and watering jars were supported outside the cages and protected in such a manner that the hen was unable to scatter feed into the collection pan. The hens seemed contented and appeared not to mind in the least the comparatively close quarters in which they were confined.

During each experiment the collection pans were cleaned daily. An extra collection pan was available and was substituted for the regular pan while the latter was being cleaned. In cleaning the pan, the frame was first freed from any excreta remaining on it by scraping the excreta into the pan below. The pan itself was then thoroughly cleaned with a steel spatula. The excreted material from each hen was kept at 0° to 4° C. in an air-tight, half-gallon glass fruit jar until the end of the experiment, when it was analyzed. In order to preserve the excreta, an equal mixture of alcohol and water, containing 10 per cent thymol, was poured over the frame each day after cleaning, the excess being caught in the pan. After running the solution over all parts of the pan, the excess was drained into the jar containing the excreta. A small amount of powdered thymol was also sprinkled over the excreta in the jars.

The procedure adopted in this investigation depended upon the fact that the excreta from chickens fed on a cereal diet normally contain little, if any, reducing sugars. This was shown by Brown (*3*) who carefully examined, by the phenyl-hydrazine test, the excreta of chickens fed on a corn diet. No trace of an osazone could be detected. Plimmer and Rosedale (*6*) found no reducing sugars in the excreta of chickens even when fed on a diet containing lactose. In the present investigation the results obtained indicate that there is no constant excretion of reducing sugars in chickens fed on a cereal diet. The determination of the completeness of utilization of ingested lactose, therefore, consisted in the analysis of the excreta for reducing sugars. In all cases the quantitative analysis was substantiated by a qualitative examination of the excreta for sugars by the formation of osazones and their identification under the microscope.

The procedure adopted for the extraction of the reducing substances in the excreta was as follows: The total excreta of each hen for the period of the experiment were extracted by pouring 200 to 500 cc. portions of hot water over the excreta in a large evaporating dish, macerating thoroughly with a pestle, and filtering through cloth. The residue in the cloth was returned to the dish and extracted again. When the total volume of the washings measured 4,000 cc., the extraction was considered complete. An extract of this volume was previously shown to be sufficient by mixing 25 gm. of lactose and 25 gm. of glucose with a seven-day collection of excreta and extracting with 200 to 500 cc. portions of hot water until the last extract failed to give a carbohydrate test with Fehling's solution. The reducing substances in the total excreta for the period of the experiment were estimated by determining the reducing substances, calculated as lactose, $C_{12}H_{22}O_{11}$, in aliquots of the thoroughly mixed extract.

Two methods were used throughout for the determination of reducing substances. The first was the combination of the Munson and Walker and the Bertrand (*2*) methods, as described by Mathews (*4, p. 994*), for the quantitative determination of reducing sugars in urine and other fluids, and the second was Benedict's (*1*) method for the estimation of glucose in urine. The first is a method of the Association of Official Agricultural Chemists [4] for the determination of reducing sugars in foods and feeding stuffs and has been found in this laboratory to be rapid and accurate. This method, however, has the disadvantage that substances other than sugars, uric acid in particular, are capable of effecting reduction of the alkaline cupric tartrate and hence, if present, would be calculated as lactose. Uric acid would, of course, be present in considerable quantities in hot aqueous extracts of chicken excreta. However, since the quantity of uric acid excreted daily from a diet in which only the amount of lactose varied would probably change but slightly, it was thought that the variation in quantity of reducing sugars present could be estimated without the previous removal of uric acid. On the other hand, the Benedict method is not appreciably affected by the presence of uric acid. Tests designed to show the effect of uric acid and to determine the applicability of the combined Munson-Walker-Bertrand and the Benedict methods to aqueous extracts of chicken excreta containing a constant amount of uric acid and varying amounts of lactose were conducted.

First, the effect of uric acid on the determination of lactose in milk by each of the two methods was tested. Lactose was determined in a sample of separated milk by the two methods in the usual manner. Then, uric acid, varying from 0.01 gm. to 1 gm. was added to 25 cc. portions of the sample and the lactose was determined by the combined Munson-Walker-Bertrand and by the Benedict methods in the usual manner with the following averaged results.

[4] ASSOCIATION OF OFFICIAL AGRICULTURAL CHEMISTS. OFFICIAL AND TENTATIVE METHODS OF ANALYSIS. As compiled by the Committee on Revision of Methods. Revised to November 1, 1919. 417 p., 18 fig. Washington, D. C. 1920. Bibliographies at ends of chapters.

TABLE I.—*Effect of uric acid on the determination of lactose by the Munson-Walker-Bertrand and the Benedict methods*

Uric acid added.	PER CENT OF LACTOSE IN SEPARATED MILK	
	Munson-Walker-Bertrand method.	Benedict method.
Gm.		
.....	4. 145	4. 152
.....	4. 106	4. 156
.....	4. 176	.....
.....	4. 192	.....
	[a] 4. 155	[a] 4. 154
0. 01	4. 200	4. 157
0. 10	4. 400	4. 150
0. 90	5. 475	4. 161
1. 00	.....	4. 173

[a] Average.

It is readily seen from Table I that uric acid markedly affects the estimation of lactose by the combined Munson-Walker-Bertrand method. In fact, where 1 gm. of uric acid was added to a 25 cc. portion of separated milk it was impossible to carry out the test. That the Benedict method is unaffected by uric acid to any appreciable extent is also shown.

In a second test about 1,200 gm. of combined excreta from four hens, fed on the standard cereal diet, were mixed thoroughly and four portions of 200 gm. each removed. To each of two portions, 25 gm. of lactose were added and the samples mixed. All four samples were then extracted in the same manner with four 300 cc. portions of hot water. Each extract was made up to 1,500 cc., mixed, and lactose determined in aliquot portions by both sugar methods in the manner in which they are used in urine analysis. The results have been averaged and summarized in Table II. Table II also contains the averaged results obtained when 1 and 2 gm. of lactose were added to excreta in a manner similar to that when 25 gm. were added. The reducing substances were determined by the Benedict method only in these cases, however.

TABLE II.—*Recovery of lactose added to excreta*

Sample of lactose.	Total reducing substances calculated as lactose.			
	Munson-Walker-Bertrand method.		Benedict method.	
	I.	II.	I.	II.
Gm.	*Gm.*	*Gm.*	*Gm.*	*Gm.*
0	0. 34	0. 35	0. 03	0. 04
25	25. 81	26. 21	24. 86	25. 13
1	[a]	[a]	1. 08	1. 11
2	[a]	[a]	2. 30	2. 21

[a] Not determined.

These tests indicated that for the purpose of this investigation either method could be used with a fair degree of accuracy. Both methods were employed throughout and the technique used was the same as that recommended for each method when applied to urine analysis. In order to obtain additional data and also to serve as a check on the quantitative results, the phenyl-hydrazine test was uniformly applied to all extracts. The osazones were examined microscopically only.

TABLE III.—*Summary of results on the utilization of lactose by the hen*

Experiment No.	Daily diet.	Hen No.	Duration of experiment.	Presence of osazones in excreta.		Total reducing substances excreted calculated as lactose, $C_{12}H_{22}O_{11}$.	
				Lactosazone.	Glucosazone.	Munson-Walker-Bertrand method.	Benedict method.
			Days.			*Gm.*	*Gm.*
I	Basal ration plus 6 gm. lactose	1	.....	−	−	1. 98	1. 70
		2	7	−	−	0. 80	0. 64
		3	.....	−	−	1. 21	0. 78
		4	.....	−	−	1. 57	1. 84
II	Basal ration plus 2 gm. lactose	1	.....	−	−	0. 00	0. 16
		2	1	−	−	0. 00	0. 03
		3	.....	−	−	0. 00	0. 03
		4	.....	−	−	0. 00	0. 15
III	Basal ration.....	1	.....	−	−	4. 34	1. 34
		2	7	−	−	3. 29	1. 40
		3	.....	−	−	0. 63	0. 60
		4	.....	−	−	1. 54	0. 72
IV	Basal ration plus 18 gm. lactose.	1	.....	−	+	5. 52	3. 89
		2	7	−	+	6. 08	3. 78
		3	.....	+	+	5. 16	4. 08
		4	.....	+	+	10. 84	7. 78
V	Basal ration.....	1	.....	−	+	3. 08	0. 56
		2	7	−	+	2. 03	1. 33
		3	.....	−	+	3. 71	1. 68
		4	.....	−	+	2. 52	1. 05
VI	Basal ration plus 24 gm. lactose.	1	.....	+	+	3. 08	1. 79
		2	7	+	+	8. 16	5. 36
		3	.....	+	+	6. 11	3. 52
		4	.....	+	+	9. 37	7. 07
VII	Basal ration.....	1	.....	−	+	2. 38	0. 70
		2	7	−	+	3. 01	1. 26
		3	.....	−	+	2. 73	0. 98
		4	.....	−	+	3. 15	1. 61

DISCUSSION

The basal ration consisted of 30 gm. of a mixture of oats and cracked corn, morning and evening, and 30 gm. of moistened mash at noon. The mash consisted of equal parts by weight of wheat bran, flour middlings, ground corn, ground oats, and tankage. The lactose fed during all the experiments was Merck's U. S. P. lactose monohydrate which proved

to be 99 per cent pure by both the Munson-Walker-Bertrand method and the Benedict method. It was fed with the mash at noon. The results are reported in grams of lactose excreted during the experiment. As would be expected from the fact that the determination of reducing sugars is affected by uric acid in the Munson-Walker-Bertrand method, while this acid does not affect, appreciably, the Benedict method, the results obtained by the latter method are, with few exceptions, much lower than those obtained by the former. On a comparative basis, however, the differences between experiments are as well shown by the one method as by the other. In the preparation of the osazones for the identification of individual sugars in the extracts the utmost care was taken, for this method of distinguishing between the sugars has never proved to be infallible in this laboratory, and especially was this found to be the case with extracts such as those dealt with in this investigation. The purified free base was used since it was found to give more satisfactory results than the hydrochlorid. While the qualitative osazone tests were not quite as satisfactory as might be desired, they confirm very well the quantitative data. In general, they indicate that lactose does not appear in the excreta of hens until comparatively large amounts are fed, that the glucosazone usually is found whenever the lactosazone is present, and that glucose persists in the excreta for some time after the lactose has disappeared.

In feeding lactose to hens it was immediately noticed that amounts exceeding 2 gm. daily caused diarrhea, a finding in agreement with that of Shaw (7). In order to test the possibility of the diarrhea itself being the cause of an increase in the excretion of reducing substances, two experiments, in which diarrhea was caused by feeding Epsom salts ($MgSO_4 . 7H_2O$) in the drinking water, were made. The results indicated clearly that the diarrhea was not the cause of the excretion of comparatively large amounts of reducing substances when lactose exceeding 2 gm. was fed.

The results of seven experiments, summarized in Table III, show that pure lactose when added to a cereal diet is utilized to a large extent by hens. All hens excreted more or less reducing substances when fed a normal cereal diet; this was, of course, expected. The amounts of reducing substances excreted by the four hens in three seven-day experiments on the lactose-free diet varied from 0.56 gm. (calculated as lactose) to 1.68 gm. by the Benedict method, as indicated in the following summary:

Hen No.	Experiment.			Average.
	III.	V.	VII.	
	Gm.	*Gm.*	*Gm.*	*Gm.*
1	1.34	0.56	0.70	0.87
2	1.40	1.33	1.26	1.33
3	0.60	1.68	0.98	1.09
4	0.72	1.05	1.61	1.13
Average				1.10

Since the method of extraction was always the same, that is, the number of extractions and the quantity and temperature of the water were exactly the same in all cases, it follows that the amounts of reducing substances excreted by each hen during the different weekly periods on the ordinary cereal diet were not constant. The average amount of reducing substances excreted by each hen during seven days was, by the Benedict method, 1.10 gm., and by the Munson-Walker-Bertrand method, 2.70 gm., expressed as lactose. If, therefore, we use these average figures as representing the grams of reducing substances originating from the basal ration in the extract of any seven-day collection of excreta, the percentages of lactose absorbed, when varying quantities of lactose were fed, may be calculated as shown in Table IV.

TABLE IV.—*Percentage absorption of lactose*

Hen No.	Percentage of lactose absorbed when the following quantities were fed—							
	2 gm.		6 gm.		18 gm.		24 gm.	
	Benedict method.	Munson-Walker-Bertrand method.	Benedict method.	Munson-Walker-Bertrand method.	Benedict method.	Munson-Walker-Bertrand method.	Benedict method.	Munson-Walker-Bertrand method.
1.....	100	100	90	100	85	85	97	98
2.....	100	100	100	100	85	82	83	77
3.....	100	100	100	100	84	87	90	86
4.....	100	100	88	100	63	55	75	73

Table IV is self-explanatory; it shows that hens will utilize lactose up to 8 gm. daily fairly completely. Attempts to feed larger quantities failed because the hens would not voluntarily eat their mash when more than 8 gm. had been mixed with it. Even when 8 gm. were fed daily it was necessary to force-feed much of the mash on the third day to all hens. This was probably due to the severe diarrhea caused by this quantity of lactose when fed in this form. Because of the severe diarrhea it was not considered wise to attempt to feed larger amounts.

The difficulties experienced in these experiments in inducing the chickens to consume large quantities of pure lactose when mixed with the feed, and the severe diarrhea always obtained when even 8 gm. a day were consumed, are in striking contrast to the experience of Plimmer and Rosedale (5). These investigators fed a diet containing secwa (a dried whey preparation containing 74.5 per cent lactose) to chickens from birth for a period exceeding four months. The amount of secwa in the diet was usually 25 per cent but in some cases was even higher. The quantity of lactose consumed in this form by each bird was as high as 22 gm. daily. Good gains were obtained and the health of the birds was excellent throughout the experiment. No reasonable explanation of these differences occurs to us.

SUMMARY

Lactose, up to 8 gm. per hen per day, was utilized fairly completely, thus making it evident that the lactose present in the quantity of whole milk, skim milk, whey, or buttermilk normally consumed (100 to 200 cc.) by chickens would be completely absorbed.

When lactose appears in the excreta, it is usually accompanied by glucose.

Lactose when fed mixed with a moist mash acts as an irritant to the gastrointestinal mucosa. Chickens will not voluntarily consume more than about 8 gm. of lactose daily when fed in the form of pure lactose mixed with the feed.

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THE OCCURRENCE OF LACTASE IN THE ALIMENTARY TRACT OF THE CHICKEN [1]

By T. S. HAMILTON and H. H. MITCHELL, *Division of Animal Nutrition, Illinois Agricultural Experiment Station.*

INTRODUCTION

In the experiments reported in the preceding paper (p. 597) it was found that lactose, fed to hens, does not appear in the excreta in appreciable quantities until excessive amounts are administered—a finding thoroughly in agreement with our present knowledge of sugar-feeding in human beings. Since lactose is assimilated from the alimentary canal of chickens, and since assimilation of disaccharids is normally preceded by hydrolysis into monosaccharids, lactase would be expected to be present in some part of the alimentary tract. However, the possibility of bacterial fermentation accounting for the disappearance of lactose must be considered.

Previous investigations are not entirely in agreement in regard to the presence of lactase in the alimentary tract of the fowl. Portier (*4* [2]) in 1898, using the osazone method for the detection of monosaccharids formed by the action of the enzym extracts on a lactose solution, found no indication of lactase in the intestines of birds. This was confirmed a year later by the extensive investigations made by Weinland (*6*) who, using the polarimetric method, found no indication of lactase in the intestines of fowls. He states, however, that the enzym is produced in the intestines of fowls if they are fed on milk and lactose. Bieri and Portier (*1*), using the duck in their experiments, found in one case, on feeding lactose and milk, that the intestines produced lactase, but a second experiment failed to confirm the first. Plimmer (*2*), in an extensive investigation on the subject of adaptation of the intestines to lactose, found that the intestines of fowls are naturally free of lactase and, furthermore, that lactase was not produced when lactose and milk were fed for long periods of time. Plimmer used Allihn's reduction method for the estimation of the degree of hydrolysis of a lactose solution produced by the enzym extracts. In a recent study on the distribution of enzyms in the alimentary canal of the chicken, however, Plimmer and Rosedale (*3*) found lactase to be present in the crop, but absent in the proventriculus and intestines. The presence of the enzym was determined by incubating at 37° C. a 4 per cent lactose solution with portions of boiled and unboiled extracts of the various organs for two days or more, removing the proteins, and determining the reducing sugars by reduction of Fehling's solution. The observed difference in reading between the boiled and unboiled solutions indicated whether or not hydrolysis by lactase had occurred. In the present investigation a similar study has been made. This inquiry did not extend, however, to the detection of lactase in the

[1] Received for publication Jan. 26, 1924.
[2] Reference is made by number (italic) to "Literature cited," p. 608.

glandular structures in the floor of the mouth nor to the gizzard, the interior lining of which resembles parchment, making the presence of secretory glands improbable.

EXPERIMENTAL DATA

The method of preparing the enzym solutions was in accordance with those usually employed. The chicken was killed either by dislocating the neck or by decapitation, and the alimentary canal immediately removed. The crop was cut open, washed out with water, and, after being cut into small pieces, was ground in a mortar with sand and a little toluene to prevent putrefaction. The entire pancreas was ground in a similar manner with sand and toluene. The proventriculus and intestine were cut open, washed out with running water, and the mucous membranes scraped off and ground in a mortar with sand and toluene. The organs from three to six chickens were used in each of three experiments. In order to control more carefully the methods used in this investigation, the small intestines of five young rats were examined in the same manner as were those of the chickens. The extracts in all cases were made by adding 75 to 125 cc. of water to the ground organs and allowing the mixture to stand at room temperature for one to three days, with occasional shaking. The mixture was then strained through cloth to remove the sand and larger pieces of the organs and the filtrate was made up to a definite volume, usually 100 or 150 cc. The presence of lactase in the extracts was determined by adding to exactly 50 cc. portions of 4 per cent lactose solution, 25 cc. of the unheated extract in one case, and, as a control, 25 cc. of the boiled extract. Three cc. of toluene were added to each flask and the flasks corked and incubated at 36° to 38° C. for two to six days. After the period of incubation, the contents of the flasks were examined for monosaccharids by means of Barfoed's copper acetate reagent. This test was made without previous precipitation of the proteins. The digested extracts were carefully filtered and the clear filtrates used. The procedure adopted consisted in adding 2 cc. portions of the boiled and unboiled digested filtrates to 5 cc. portions of the copper acetate reagent and placing the resulting solutions in boiling water for exactly five minutes. The test was considered negative if no reduction was apparent during the five minutes boiling or during the three minutes after removal from the water bath. All tests were run in duplicate and the solutions containing the boiled and unboiled extracts were run side by side, at the same time and in exactly the same manner. The results obtained are summarized in Table I.

TABLE I.—*Distribution of lactase in the alimentary tract of the chicken*

Part of the alimentary tract used.	Number of chickens from which organs were composited.	Number of experiment.	Barfoed's test for monosaccharids.			
			Unboiled sample.		Boiled sample.	
			I.	II.	I.	II.
Crop	3	1	+	+	−	−
Do	3	2	+	+	−	−
Do	6	3	+	+	−	−
Proventriculus	4	1	−	−	−	−
Do	3	2	−	−	−	−
Do	6	3	−	(?)	−	−
Pancreas	4	1	−	−	−	−
Do	3	2	−	−	−	−
Do	6	3	−	−	−	−
Intestine	4	1	(?)	(?)	−	−
Do	3	2	−	−	−	−
Do	6	3	−	−	−	−
Small intestines from five rats		4	+	+	−	−

DISCUSSION

Roaf (5) has shown that Barfoed's copper acetate reagent can be used with accuracy in testing the hydrolysis of disaccharids to monosaccharides by enzyms if a boiled control is run at the same time and in exactly the same manner as the unboiled solution. Preliminary experiments with this reagent and with two quantitative reduction methods, the Munson-Walker-Bertrand combination and the Allihn method, indicated that the qualitative copper acetate reagent could be used most accurately and advantageously with this type of solution. The chief disadvantages of any quantitative method lie in the fact that the difference in the reducing power of lactose and of hydrolyzed lactose is small. Slight errors in measurement of solutions might easily make consistent differences in the amount of reduction, which might indicate hydrolysis. When the lactose is only partly hydrolyzed, the difference in reduction would be still less, and when the sugar solution is very dilute the results obtained by the quantitative reduction methods can not be considered satisfactory. Examination of the table will show uniformly negative reductions in all lactose solutions containing the boiled enzym extract. This is a further check on the accuracy of the method, the absence of reduction in these tubes proving that any reduction taking place in the unboiled extract tubes was due only to the hydrolytic action of an enzym and not to any other treatment such as the reaction of the solutions or boiling.

As shown by the table, the unboiled extracts of the crop showed an unquestionable reduction of the copper acetate reagent and, consequently, the presence of lactase. The unboiled extracts from neither the proventriculus, the pancreas, nor the intestines of the chickens gave any signs of reduction, with the exception of three questionable results, which are indicated in the table by question marks. These results were questioned because, while a very slight brownish coloration was obtained, it was not sufficient to be considered a positive test, and at the same time was different from the corresponding boiled extracts. Compared with the

amount of reduction obtained in the case of the unboiled extracts of the small intestines of young rats, the unboiled crop extracts of chickens showed considerably less reduction. These results were an unexpected confirmation of the results of Plimmer and Rosedale (*3*), who found lactase in the crop of chickens but in no other part of the alimentary tract.

SUMMARY

Lactase was found to be present in the crop but absent in the proventriculus, the pancreas, and the intestines of normal chickens.

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THE LIFE HISTORY OF THE GRAPE ROOTROT FUNGUS ROESLERIA HYPOGAEA THÜM. ET PASS.[1]

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INTRODUCTION

The fungus *Roesleria hypogaea*, associated with a rootrot of grapes, has long been known, especially in the grape-growing regions of Europe. It has not been definitely proved that this fungus is the primary cause of the rot, but there is no question that, once established, it contributes largely toward the killing of the roots. Disagreement among mycologists as to the identity of some well-known fungus is often due to a lack of knowledge of its life history. Confusion has more than once arisen because of an accidental similarity of fruit bodies or spores. A case in point is that of Roesleria and Pilacre.

We are indebted to Brefeld (*5*[2]) for the beautiful illustrations of *Pilacre petersii* B. & C., a fungus which he believed to represent a very primitive Basidiomycete. His figures of the fruiting bodies on bark show a "gleba" composed in part of short septate branches, each bearing a definite number of spores. Such a branch he considers a simple basidium. *Roesleria hypogaea* Thüm. and Pass., an ascogenous fungus whose fruiting bodies have a strong superficial resemblance to those of *P. petersii*, is, on this account, most interesting. *Calicium pallidum* Pers., well known to lichenologists, also has fruiting bodies similar in general appearance to those of Roesleria and *P. petersii*. Since Rehm (*27, p. 396*) considers *Coniocybe pallida* (Pers.) Fr. a synonym of *R. hypogaea*, and Bayliss-Elliott and Grove (*8*) suggest that *R. hypogaea* is merely the ascogenous stage of *P. petersii*, and since Viala and Pacottet (*35*) report conidial and chlamydosporic forms of Roesleria in culture, it is not surprising that we find the greatest confusion of these names in the literature. The writer has had the opportunity recently to study *R. hypogaea* and *P. petersii* in culture and has also compared them with specimens of the lichen, *Coniocybe pallida*, with the result that we find that there is no basis for considering these fungi identical or genetically related.

From a review of the literature it will be seen that the grape rootrot fungus has been described under a number of different names and combinations. The following list includes such as appear from original descriptions and illustrations to refer to a Discomycete identical with *Roesleria hypogaea* of von Thümen and Passerini.

Pilacre subterranea Wein. 1832. (*36, p. 458.*)
Pilacre friesii Wein. (*in* Flora) 1832. (*36, p. 458.*) Not Wein. 1834.
Onygena friesii Wein. 1834. (*37, p. 413–414.*)
Vibrissea flavipes Rab. 1852. (*26, p. 286.*)
Sphinctrina coremioides B. & Br. 1872. (*2*).
Roesleria hypogaea Thüm. & Pass. 1877. (*32.*)

[1] Received for publication Nov. 23, 1923.
[2] Reference is made by number (italic) to "Literature cited, pp. 615–616."

Vibrissea hypogaea (Thüm. & Pass.) Rich. 1881. (*28.*)
Coniocybe pilacriformis Rehm 1892. (*20, p. 56.*)
Roesleria pilacriformis (Rehm) Henn. 1895. (*16.*)
Pilacre pilacriformis (Rehm) Boud. 1907. (*4.*)
Pilacre pallida Boud. 1907. (*4.*) Not *Calicium pallidum* Pers. 1794 (*23, p. 20*), nor *P. pallida* E. & E. 1900. (*9, p. 59.*)

A lichen *Calicium pallidum* Pers. 1794 (*23, p. 20*), (*Coniocybe pallida* (Pers.) Fr. 1824 (*11, I, p. 3*), has also been confused with *Roesleria hypogaea.* The specific name "pallida" has been used frequently in combination with the generic name Roesleria (*R. pallida* (Pers.) Sacc. (*30, p. 299*) to refer to a fungus thought at the time to be one of the Stilbaceæ but which is in reality *Roesleria hypogaea.*

Another fungus, nonascogenous, commonly called *Pilacre faginea,* or *P. petersii* in this country, has been regarded erroneously by various authors as a conidial stage of *Roesleria hypogaea.* It appears to have been first described as *Onygena faginea* Fr. The synonomy of this fungus so far as can be ascertained by a study of original descriptions and the literature is as follows:

Onygena faginea Fr. 1818. (*10, p. 25.*)
Onygena decorticata Schwein. 1822 (*31, p. 65.*) Not *Onygena decorticata* Pers. 1799. (*24.*)
Phleogena faginea (Fr.) Link 1833. (*21, p. 396.*)
Pilacre friesii Wein. in Linnaea. 1834. (*37, p. 413–414.*) (Not *P. friesii* Wein. *in* Flora 1832. (*36, p. 458.*)
Botryochaete faginea (Fr.) Corda 1854. (*7, pl. 9, fig. 95.*)
Pilacre faginea (Fr.) B. & Br. 1850. (*3, v. 5, p. 365, pl. 11, fig. 5.*)
Ecchyna faginea Fr. 1857. (*13, p. 151.*)
Pilacre petersii B. & C. 1859. (*3, v. 3, p. 362.*)
Stilbum pilacriforme Rich. 1889. (*29*), not *Coniocybe pilacriformis* Rehm (*20, p. 56*).

The grape rootrot fungus has been reported growing on the roots of various hosts such as Vitis, Malus, Pyrus, Cydonia, Prunus (almond and cherry), Salix, Tilia, Rosa, and Paliurus.

From a résumé of the literature, it would seem that the advocates of the parasitic nature of Roesleria as opposed to its saprophytic nature of growth are almost evenly divided. The following consider it parasitic: Lemonnier (*19*), d' Arbois de Jubainville (*1*), Hennings (*16*), Jolicoeur (*17, p. 219–224*), Massee (*22, p. 289*), and Bayliss-Elliott and Grove (*8*). Gillot (*14*), von Thümen (*33, p. 210–212*), and Prillieux (*25*) believe it to be somewhat parasitic, while it is thought to be nonparasitic by Berkeley (*2*), Cooke (*6*), Laurent (*18*), Viala and Pacottet (*35*), Hartig (*15, p. 83*), and Verge (*34*). The results of the writer's experiments show that when ascospores are sown in wounds the fungus can establish itself in living roots.

CULTURES

Cultures were made on various media from ascospores from the fruiting bodies of Roesleria on apple roots (Pl. 1, A) collected in New York City in October, 1920, by Dr. Dodge.[3] Plates of cleared corn-meal agar were

[3] DODGE, B. O. A ROOT-ROT DISEASE OF APPLE SEEDLINGS. (Title) *In* Amer. Assoc. Adv. Sci. Program. 71st meeting, p. 32. 1918. A number of French crab-apple seedlings, obtained through a nursery, had been grown in pots for two years, then set out in the garden. During this time the plants had been inoculated with the pear-blight organism, and had been attacked somewhat by wooly aphids in the garden. Early in November in 1917 it was noticed that several of the little trees were falling over, due to the fact that their root systems had been destroyed by some rot. By digging down in the soil a few inches, partially decayed pieces of roots were found bearing numbers of ascocarps of Roesleria. The greenish mycelium of the fungus was discovered at least a foot beneath the surface of the ground. Fruiting bodies of the fungus were found on roots of plants the remainder of the root systems of which appeared to be perfectly healthy.

inoculated on October 18, 1920, with ascospores from the fruiting heads. In two days numerous spores germinated. Growth was slow, the germ tubes having reached a length of not more than 20μ. Viala and Pacottet (*35*) described fairly accurately the method of germination, showing that a few spores became septate during germination but more of them were undivided. Single spores were marked in the plates, and when they had germinated each spore was transferred to a tube of slanted corn-meal agar. All of the writer's cultures discussed in this paper were derived by transfer from these single ascospore cultures. Eight single spore cultures were made and kept at room temperature until the mycelium had made good growth, and they were then placed in a refrigerator where the temperature averaged 10 to 12° C. This provided uniformly cool, moist and dark conditions for growth.

CORN-MEAL AGAR CULTURES

On the corn-meal agar the fungus grows slowly forming a thin layer of felty mycelium, white to buff at first, becoming green at the center, the green color gradually spreading over the surface. It becomes blackish green with age, sometimes taking on a grayish tinge. None of these first transfers fruited, but later transfers were made to the same medium, making in all 28, and at the end of five months stalked fruiting bodies were found on three cultures, one culture having three at the base of the agar. These were small and white or grayish white ascocarps with heads scarcely wider than the stalks. The heads contained asci and paraphyses which were slender and extended out beyond the asci.

OATMEAL PASTE AGAR CULTURES

Agar in which the nutrient medium is an oatmeal paste was found very satisfactory for the development of Roesleria. Forty-five transfers were made at different times from single ascospore cultures to tubes of this medium; 37 of these were kept at least part of the time in the refrigerator at 10° to 12° C. The mycelium spreads very slowly, forming a compact growth, cream or buff colored at first which becomes a bright malachite green, darkening with age. The growth is more felty, more luxuriant, and of a brighter green than that on the corn-meal agar. In from five to seven months ascocarps appeared in a large number of the tubes. They occurred singly or in groups of from 2 to 15 (Pl. 1, B, F, G). The stalks were white to grayish with mouse-gray heads. These fruiting bodies, 4 to 4½ mm. × 1 mm. were somewhat larger than those occurring in nature on the roots, the stalk being thicker and the heads larger, 3 mm. wide in the largest ones.

CULTURES ON APPLE ROOTS

Transfers were made from each of the single-spore cultures to autoclaved apple roots in large test tubes, with a few cubic centimeters of water in the bottom. These cultures were kept in the refrigerator at 10 to 12° C. The fungus grew well, covering the roots with a felty or fluffy mycelium, white to buff at first, later becoming bright malachite or fluorite green (Ridgway).[4] In from 6 to 12 months, when the cultures had dried somewhat, fruit bodies containing mature asci appeared

[4] RIDGWAY, Robert.—COLOR STANDARDS AND COLOR NOMENCLATURE. 43 p., 53 col. pl. Washington, D. C. 1912.

singly or more often in groups (Pl. 1, C, E). As many as 14 ascocarps developed in one group. The larger ascocarps developed to maturity, but some of the smaller ones had not matured by the time the cultures dried.

CULTURES ON RUBUS STEMS

Four similar tubes containing blackberry stems with a few leaves were sterilized, inoculated, and treated in the same manner as previously described for apple roots. The mycelium which developed was light to dull green and felty but less luxuriant than on the apple roots. The cultures fruited sparingly, one having several small ascocarps on the midrib of a leaf, another with several fruiting in different stages of development at the base of the stem. Even the smallest ascocarps matured.

CULTURES MADE FOR COMPARISON WITH THOSE OF VIALA AND PACOTTET

In view of the fact that in the writer's cultures described above ascocarps were developed without the fungus producing any intermediate spore forms such as the conidia reported by Viala and Pacottet (*35*), she has endeavored to grow the fungus in such a way as to duplicate as nearly as possible the cultures described by them. The writer's methods were as follows: Two 2-liter flasks were filled to a depth of 6 or 7 cm. with kidney-bean juice with $\frac{1}{10}$ per cent tartaric acid and 5 per cent sugar added. (The fungus did not grow on media made with 1 per cent tartaric acid as specified by Viala and Pacottet.) These were steamed for three successive days. They were inoculated with bits of mycelium from single ascospore cultures. No. 1 was kept in the light at room temperature averaging 20 to 25° C., No. 2 was treated in the same way for five months, then put into a refrigerator with temperature at about 10 to 12° C. About a week after inoculation, one colony grew on the surface of each and within a day or two showed a greenish color. These colonies soon appeared warty, raised at the edges, and depressed in the center, which was yellowish green. Around the colonies the liquid was iridescent, forming a film. A month or so later the colonies appeared heavy and fell to the bottom. In flask No. 1 the colony grew considerably and formed numerous rounded protuberances covered with whitish mycelium, giving them a fluffy appearance. Some of the nodules were as large as 1 to 1½ cm. in diameter. The main part of the colony was dark, with some brownish accretions or precipitate from the liquid. Several months later flask No. 2, which had been in the refrigerator for some time, showed 12 or 15 immersed colonies, while the other flask had only 3 or 4. Some had greenish to deep-green zones, while one or two appeared deep green and warty only at the center. None of the colonies adhered to the glass, as was the case in Viala and Pacottet's cultures, but all remained separate and free in the liquid. They were subspherical or hemispherical, but had no stalks such as they describe. Microscopically, all showed mycelium with numerous rounded subhyaline swellings, often occurring singly or in rows of 3 or 4. The mycelium was of a slightly yellowish or yellowish-brown tinge. Viala and Pacottet called these bodies chlamydosporic fruits, and the rounded swellings chlamydospores. It is a well-known fact that the mycelium of many species of fungi which grow for a long time in culture becomes abnormal, and the cells become misshapen so as to resemble chlamydospores. Viala and Pacottet did

not show that they function as spores in any way. While the writer did not find these bodies quite so regularly developed in long chains as described by these authors, there can be no doubt that they are identical.

One 2-liter flask of kidney-bean juice with 2 per cent agar and pieces of steamed grapevine added was autoclaved and inoculated with bits of mycelium from a single-spore culture. In a few days compact round colonies buff in color appeared. These increased in size and when about one-half inch in diameter were raised in the center, felty, and pale green with rim of white or buff. The green color deepened and brightened, and when the colonies were 5 cm. across they were deep grayish green with wide white or cream colored margins. The colonies coalesced with distinct lines of demarkation. Soon concentric rings appeared with the centers glaucous, green, and felty. The other rings were in order, buff color and white, the newest growth being white. The whole growth was superficial, and no fruiting bodies of any kind were ever formed.

Another 2-liter flask of kidney-bean juice containing 4 per cent agar with $\frac{1}{10}$ per cent tartaric acid and 5 per cent sugar with pieces of steamed grape vine added was inoculated in the same way as the other flasks. This medium had a jelly-like consistency. Seven or eight compact felty buff-colored colonies appeared in less than two weeks, one showing a faint greenish-brown tinge. Two or three weeks later the colonies were quite irregular, felty, and greenish yellow, with wide white or buff colored margins, which soon coalesced. No fruiting bodies or chlamydospores were formed on this medium. Viala and Pacottet report that their cultures on similar media produced conidia.

INOCULATION OF GRAPE ROOTS

A number of roots of grape were inoculated in April, 1921, by placing mycelium in wounds made on the roots or by spraying them with ascospores produced in culture. A number of fruiting bodies were found eight months later on certain roots which had been sprayed with ascospores. These fruiting bodies were characteristic ascocarps, except that some of them had greenish stalks and heads, while some were buff colored with cinder-gray heads. They produced asci and ascospores of the usual sort.

DISCUSSION

The results of the culture experiments show that ascocarps were formed on all the media in tube cultures after four or five months, 37 cultures fruiting. None has been found in the large flasks of kidney-bean media, but these cultures comprised a much larger bulk and remained in a moist condition, and up to the time reported on were not dried down, as were the test-tube cultures. Ascocarps were developed abundantly in cultures from single ascospores and without any intermediate spore form such as *Pilacre petersii* or other imperfect stage. The best medium for the production of fruiting bodies was obtained by autoclaving apple roots in test tubes. These were large tubes giving a good supply of air, and when the culture medium had dried somewhat fruiting bodies formed in abundance. Rubus stems used in the same way proved much less satisfactory, while oatmeal-paste agar was second only to apple roots, and these cultures could be depended on to produce numerous ascocarps. A cool, humid atmosphere, such as obtains in the ordinary refrigerator, was apparently essential to the production of fruiting bodies. At room temperature in diffuse light only one culture was found with ascocarps.

Viala and Pacottet (*35*) report that they had no success whatever in germinating ascospores in culture. They used ascospores which germinated on heads developed from the old mycelium in roots kept several months in damp chambers. This method would open the way for contamination. The writer's cultures were all obtained from single ascospores germinated in Petri dishes and transferred each to a tube of nutrient agar; later cultures were obtained by transfer from these. Viala and Pacottet found no difference in the color of the mycelium on the different media used, all having shown a malachite green. The writer found this green color fairly constant except on the kidney-bean media to which tartaric acid and sugar were added. In this medium a slight green color was observed in the early stages of growth, but for the most part a greenish-yellow color obtained, noticeable particularly on the solid medium and to some extent in the liquid medium. The only yellow color mentioned by Viala and Pacottet was in connection with what they thought were conidiophores, which they noted were white to yellowish in the early stages, and their "chlamydosporic fruits" which were yellow when young. The conidiophores described by them in some of their older cultures have not been observed in the writer's cultures at any time, although some of them are more than two years old. As for the chlamydosporic fruits of Viala and Pacottet, structures with such appearances are often found in old cultures of fungi and have no significance.

SUMMARY AND CONCLUSIONS

Whether the name Pilacre should be applied to an ascomycete or not is impossible to say until the nature of Fries' specimen of *P. weinmanni* is known (*12*). Without such an investigation, just as pointed out by Bayliss-Elliott and Grove (*8*), any attempt to settle definitely the question of priority with regard to the names which have been applied to the grape and apple rootrot fungus would be premature.

The Roesleria of von Thümen (*32*) is an ascomycete which can be grown easily in culture from ascospore to ascospore. The spores are sometimes septate on germination, producing one or two germ tubes. This fact has led some to suggest that it belongs in the family Geoglossaceae. A fine septate felty mycelium is formed, which both in culture and frequently on the roots shows a characteristic malachite green. Ascocarps are formed in culture in the refrigerator, where the dark, cool conditions simulate the natural soil conditions where ascocarps mature in the fall of the year. Notwithstanding the fact that ascocarps were frequently formed only after the agar had dried out considerably, this dryness is clearly not a necessary condition, because fruit bodies were formed sometimes on the weft of hyphae floating on the water in the bottom of the test tubes containing sterilized roots which were used instead of an agar medium (Pl. 1, D). The strain from apple rootrot is evidently the same as that found on grape, since inoculations of grape roots with the strain from apple have resulted in the formation of similar ascocarps.

In discussing the relationship between Pilacre and Roesleria, Bayliss-Elliott and Grove (*8*) state:

> Moreover it became evident that it would do no violence to the facts if it were concluded that *Pilacre faginea* and *P. petersii* were also identical with each other, and that both resembled the Roesleria so much in character as to make it seem not unlikely that Pilacre is only a stage of Roesleria.

And later:

> The conclusion at which we have arrived is that Pilacre is a conidiophorous fungus, not in any sense a Basidiomycete, and that it is not in the remotest degree allied to the Auricularieae and Tremellineae, but is a stage of the Discomycetous genus Roesleria.

This suggestion can no longer be entertained. No conidial stage has ever appeared in the life cycle of Roesleria which the writer has grown to maturity many times in single ascospore cultures. Conidia are produced freely in cultures of the Basidiomycete *Pilacre petersii*. Roesleria is hypogaeous, developing large quantities of ascospores which can not be discharged into the air in any way comparable to that prevailing in most other Ascomycetes, the asci deliquesce allowing the spores to mass together in the head, which is at first covered with a peridium-like weft of hyphae. This is soon broken away by the crowding of the spores. Spore distribution is probably brought about by disturbances of the soil by insects, earthworms, or by cultivation.

It has been pointed out that there are three distinct fungi having fruit bodies which are more or less similar in appearance: One, a lichen growing on bark, *Calicium* (*Coniocybe*) *pallidum;* another, a Discomycete growing on roots, *Roesleria hypogaea;* and third, *Pilacre petersii*, the primitive Basidiomycete of Brefeld. If Pilacre is an ascogenous genus, *P. petersii* does not belong with it. Certainly *R. hypogaea* is not a lichen. There is no basis for considering either *Coniocybe pallida* or *Pilacre petersii* synonymous with *Roesleria hypogaea.*

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PLATE 1

A.—Ascocarps of *Roesleria hypogaea*, collected October, 1920, on root of French crab seedling grown in the garden of Columbia University, New York City. The writer's cultures were obtained from ascospores from this specimen.

B.—Culture of Roesleria on oatmeal paste in tube showing ascocarps, 10 months after inoculation. Natural size.

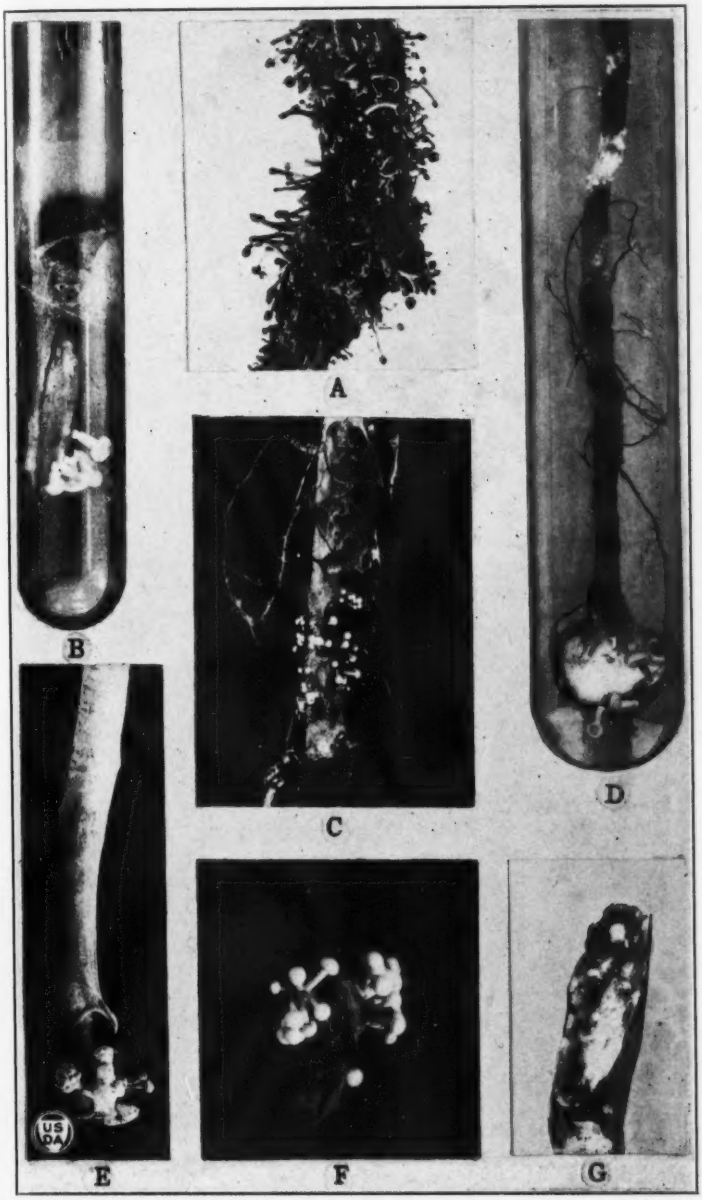
C.—Apple root from tube culture showing numerous small ascocarps, 9 months old. Slightly magnified.

D.—Apple root in tube showing ascocarps produced on the hyphal weft formed on the water at the bottom. Culture scarcely 5 months old. Natural size.

E.—Apple root from tube culture showing a group of ascocarps somewhat older (9 months). The "peridium" in each has broken away. × 1.4.

F.—Oatmeal paste agar culture removed from the tube showing groups of large ascocarps. Culture a year old. × 1.4.

G.—Oatmeal paste agar culture removed from the tube showing ascocarps on upper part of slant. Culture 5 months old. Natural size.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